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E. BRUCE GOLDSTEIN • LAURA CACCIAMANI

Sensation & Perception

11th Edition

ELEVENTH EDITION

Sensation and Perception

E. Bruce Goldstein

University of Pittsburgh

University of Arizona

and

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Eleventh Edition
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Laura Cacciamani

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Cover Designer: Bethany Bourgeois

Cover Image Source: iStockphoto.com/ Chris LaBasco

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WCN: 02-300

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Library of Congress Control Number: 2021900075

Student Edition:
ISBN: 978-0-357-44647-8

Loose-leaf Edition:
ISBN: 978-0-357-44648-5

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200 Pier 4 Boulevard
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Printed in the United States of America
Print Number: 01 Print Year: 2021

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Bruce Goldstein

To Barbara: It's been a long and winding road, but we made it all the way to the 11th edition! Thank you for your unwavering love and support through all of the editions of this book.

I also dedicate this book to the editors I have had along the way, especially Ken King, who convinced me to write the book in 1977, and also those that followed: Marianne Taflinger, Jaime Perkins, and Tim Matray. Thank you all for believing in my book and supporting its creation.

Bruce Goldstein

Sarah Williams

To Zack, for supporting me through the winding roads of academia and listening to me ramble about research on many, many occasions.

And to my mother, Debbie, for being my life-long role model and demonstrating what it means to be a compassionate, persevering, independent woman.

Laura Cacciamani

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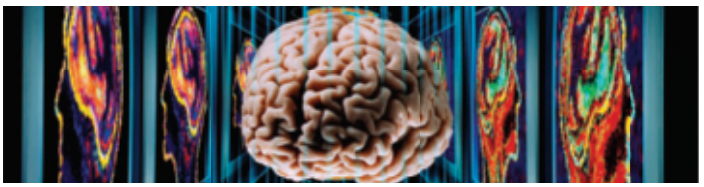

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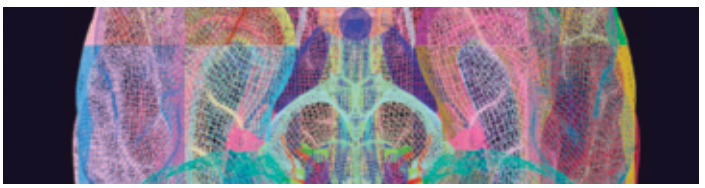

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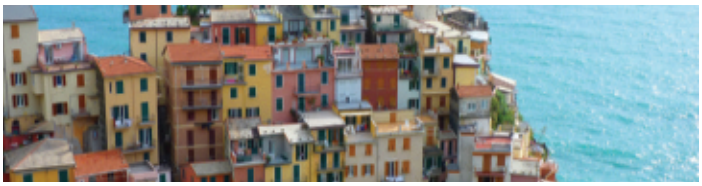

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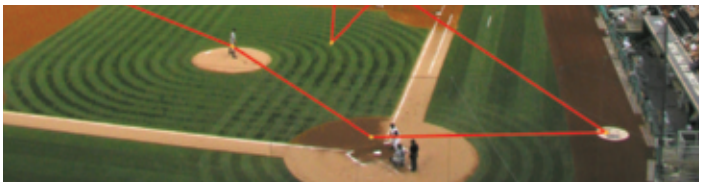

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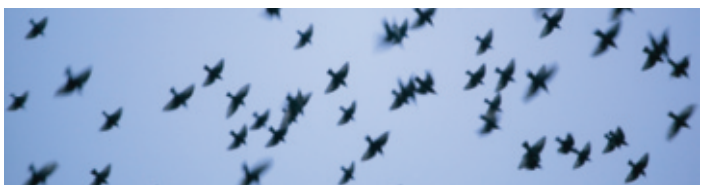

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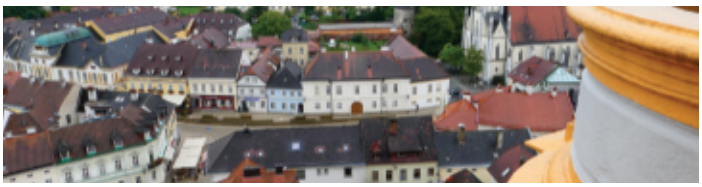

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Preface

by Bruce Goldstein

A long, long time ago, Ken King, the psychology editor of Wadsworth Publishing Co., knocked on the door to my office at the University of Pittsburgh, came in, and proposed that I write a textbook titled *Sensation and Perception*. This led me to begin writing the first edition of *Sensation and Perception* in 1977, the year *Star Wars* made its debut in theaters and when the first mass-market personal computer was introduced.

While Luke Skywalker was dealing with Darth Vader and was working to master the Force, I was dealing with understanding the perception literature and was working to present the results in this literature as a story that would be both interesting to students and would help them understand how perception works.

How do you tell a story in a textbook? This is a problem I grappled with when writing the first edition, because while the textbooks available at that time presented "the facts," they did so in a way that wasn't very interesting or inviting to students. I decided, therefore, that I would create a story about perception that was a narrative in which one idea followed from another and that related the results of research to everyday experience—a story describing both the historical background behind scientific discoveries and the reasoning behind scientific conclusions. The result was the first edition of *Sensation and Perception*, which was published in 1980 (**Figure P.1**). The book was popular, largely because of my decision to present not just facts, but also to present the story and reasoning behind the facts.

The producers of *Star Wars* had no idea, when they released their first movie, that it would give birth to a franchise that is still alive today. Similarly, I had no idea, when the first edition of *Sensation and Perception* was published, that it would be the first of 11 editions.

The book you are reading was, in a sense, born as the first edition was being written in 1977. But a lot has happened since then. One indication of this is the graph in **Figure P.2**, which plots the number of references in this edition by decade. Most of the references to the left of the dashed line appeared in the first edition. The ones to the right were published after the first edition.

Another measure of the evolution of this book is provided by the illustrations. The first edition had 313 illustrations. Of these, 116 have made it all the way to this edition (but transformed from black and white into color). This edition has 440 illustrations that weren't in the first edition, for a total of 556.

But enough history. Most users of this book are probably more interested in "what have you done for the book lately?" Returning to illustrations, 90 of the illustrations in this edition

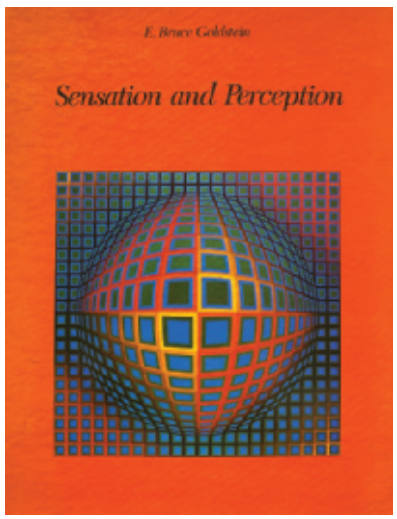

Figure P.1 The cover of the first edition of *Sensation and Perception* (1980), which featured a reproduction of the painting *Vega-Nor 1960*, by Victor Vasarely, from the Albright-Knox Art Gallery, Buffalo, New York.

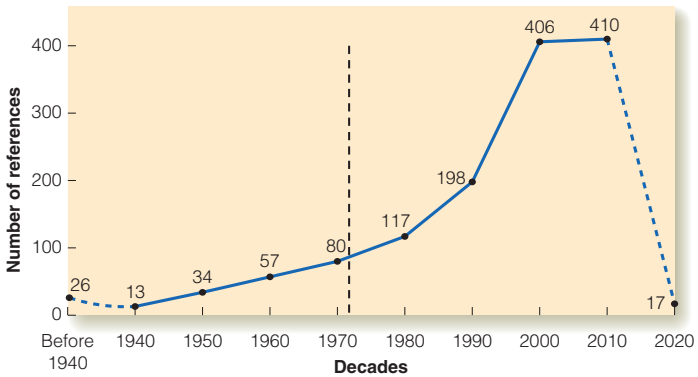

Figure P.2 The number of reference citations in this edition, by decade. For example, 1970 includes all references dated from 1970 to 1979. This means that all of the references to the right of the dashed vertical line appeared 1980 or after, and so were in editions after the first edition. The line on the right is dashed because it connects to 2020, which includes references only from 2020 and the beginning of 2021, not a whole decade.

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are new since the 10th edition. There's much more that's new since the 10th edition when it comes to content, which I'll get to shortly. But first, one of the most important things about this edition is that it still contains the popular content and teaching features that have been standbys for many editions. These features are as follows:

Features

The following features focus on student engagement and learning:

- **Learning Objectives.** *Learning Objectives,* which provide a preview of what students can expect to learn from each chapter, appear at the beginning of each chapter.
- **Test Yourself.** *Test Yourself* questions appear in the middle and at the end of each chapter. These questions are broad enough that students have to unpack the questions themselves, thereby making students more active participants in their studying.
- **Think About It.** The *Think About It* section at the end of each chapter poses questions that require students to apply what they have learned and that take them beyond the material in the chapter.

The following feature enables students to participate in perceptual activities related to what they are reading:

- **Demonstrations.** *Demonstrations* have been a popular feature of this book for many editions. They are integrated into the flow of the text and are easy enough to be carried out with little trouble, thereby maximizing the probability that students will do them. See list on page xv.

The following features highlight different categories of material:

- **Methods.** It is important not only to present the facts of perception, but also to make students aware of how these facts were obtained. Highlighted *Methods* sections, which are integrated into the ongoing discussion, emphasize the importance of methods, and the highlighting makes it easier to refer back to them when referenced later in the book. See list on page xiv.
- **Something to Consider.** This end-of-chapter feature offers the opportunity to consider especially interesting phenomena and new findings. A few examples include The Puzzle of Faces (Chapter 5), Focusing Attention by Meditating (Chapter 6), The Changing Moon (Chapter 10), and Community of the Senses (Chapter 16).
- **Developmental Dimensions.** The *Developmental Dimension* feature, which was introduced in the ninth edition, has proven to be popular and so has been continued and expanded in this edition. This feature, which appears at the end of chapters, focuses on perception in infants and young children.

The following feature provides digital learning opportunities that support the material in the text:

- ***MindTap*** *for Sensation and Perception* engages and empowers students to produce their best work—consistently. For those courses that include MindTap, the textbook is supplemented with videos, activities, apps, and much more. MindTap creates a unique learning path that fosters increased comprehension and efficiency.

  For students:

- MindTap delivers real-world relevance with activities and assignments that help students build critical thinking and analytic skills that will transfer to other courses and their professional lives.
- MindTap helps students stay organized and efficient with a single destination that reflects what's important to the instructor, along with the tools students need to master the content.
- MindTap empowers and motivates students with information that shows where they stand at all times—both individually and compared to the highest performers in class.

  Additionally, for instructors, MindTap allows you to:

- Control what content students see and when they see it with a learning path that can be used as is, or matched to your syllabus exactly.
- Create a unique learning path of relevant readings, multimedia, and activities that move students up the learning taxonomy from basic knowledge and comprehension to analysis, application, and critical thinking.
- Integrate your own content into the MindTap Reader, using your own documents or pulling from sources like RSS feeds, YouTube videos, websites, Google Docs, and more.
- Use powerful analytics and reports that provide a snapshot of class progress, time in course, engagement, and completion.

In addition to the benefits of the platform, *MindTap for Sensation and Perception* includes:

- **Exploration.** The MindTap *Exploration* feature enables students to view experimental stimuli, perceptual demonstrations, and short film clips about the research being discussed. These features have been updated in this edition, and new items have been added to the labs carried over from the ninth edition.

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Most of these items have been generously provided by researchers in vision, hearing, and perceptual development.

New to This Edition

This edition offers many improvements in organization, designed to make the text read more smoothly and flow more logically. In addition, each chapter has been updated to highlight new advances in the field, supported by many new references. Here are a few examples of changes in this edition.

Key Terms New to This Edition

The following key terms represent methods, concepts, and topics that are new to this edition:

Aberration
Action affordance
Adaptive optical imaging
Adult-directed speech
Affective function of touch
Alzheimer's disease
Arch trajectory
Automatic speech recognition (ASR)
Cloze probability task
COVID-19
Dopamine
Duple meter
Early right anterior negativity (ERAN)
Experience sampling
Figural cues
Functional connectivity
Hand dystonia
Head-mounted eye tracking
Interpersonal touching
Meditation
Metrical structure
Microneurography
Mild cognitive impairment
Mind wandering
Multimodal interactions
Munsell color system
Music-evoked autobiographical memory (MEAM)
Musical phrases
Novelty-preference procedure
Odor-evoked autobiographical memory
Predictive coding
Predictive remapping of attention
Seed location
Semitone
Social pain
Social touch
Social touch hypothesis
Sustentacular cell
Syncopation
Syntax, musical
Task-related fMRI
Temporal structure
Triple meter

Revisions and New Material

Each chapter has been revised in two ways: (1) Organization: Chapters and sections within chapters have been reorganized to achieve smoother flow from one idea to the next; (2) Updating: Material describing new experimental results and new approaches in the field has been added. New "Developmental Dimensions" topics are indicated by DD and new "Something to Consider" topics by STC.

Perceptual Principles (Chapters 1–4)

The initial chapters, which introduce basic concepts and research approaches, have been completely reorganized to make the opening of the book more inviting to students, to create a more logical and smooth flow, and to include all of the senses up-front. Discussing a number of senses in Chapter 2 corrects a problem perceived by some teachers, who felt that the opening of the 10th edition was too "vision-centric." Chapter 2 also contains a new section discussing structural and functional connectivity.

Perceiving Objects and Scenes (Chapter 5)

- Updated section on computer vision
- Predictive coding
- Pre-wiring of functional connectivity for faces in human infants

Visual Attention (Chapter 6)

- Predictive remapping of attention
- Mere presence of smartphones can negatively impact performance.
- Head-mounted tracking devices to measure infant attention
- STC: Focusing Attention by Meditating
- DD: Infant Attention and Learning Object Names

Taking Action (Chapter 7)

- New material on proprioception
- Hippocampus-related navigation differences in non-taxi drivers
- STC: Prediction Is Everywhere
- DD: Infant Affordances

Perceiving Motion (Chapter 8)

- Changes in motion perception over the first year
- Motion and social perception
- STC: Motion, Motion, and More Motion

Perceiving Color (Chapter 9)

- Color and judging emotions of facial expressions
- Reevaluation of the idea of "unique hues"
- Social functions of color
- Color areas in cortex sandwiched between face and place areas
- #TheDress and what it tells us about individual differences and color constancy
- Novelty-preference procedure for determining infant color categorization

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Perceiving Depth and Size (Chapter 10)

- Praying mantis cinema used to test binocular depth perception
- STC: The Changing Moon

Hearing (Chapter 11)

- STC: Explaining Sound to an 11-Year-Old

Hearing in the Environment (Chapter 12)

- Human echolocation
- STC: Interactions Between Hearing and Vision

Perceiving Music (Chapter 13)

- New chapter, greatly expanding coverage of music, which was part of Chapter 12 in the 10th edition
- Music and social bonding
- Therapeutic effects of music
- Infant emotional response to music
- Chemistry of musical emotions
- Effect of syncopation on music-elicited movement
- Cross-cultural similarities
- Music and prediction
- Behavioral and physiological differences between music and speech
- DD: How Infants Respond to the Beat

Perceiving Speech (Chapter 14)

- Role of motor processes in speech perception
- STC: Cochlear Implants
- DD: Infant-Directed Speech

The Cutaneous Senses (Chapter 15)

- Social touch and CT afferents
- Cortical responses to surface texture
- Top-down influences on social touch
- Pain reduction by social touching
- Pre- and post-partum touch perception
- STC: Plasticity and the Brain
- DD: Social Touch in Infants

The Chemical Senses (Chapter 16)

- Comparing human and animal perception of scent
- Music can influence flavor
- Color can influence flavor
- Odors can influence attention and performance
- Loss of smell in COVID-19 and Alzheimer's
- STC: Community of the Senses

Acknowledgments

It is a pleasure to acknowledge the following people who worked tirelessly to turn the manuscript into an actual book. Without these people, this book would not exist, and both Laura and I are grateful to all of them.

- Cazzie Reyes, Associate Product Manager, for providing resources to support the book.
- Jacqueline (Jackie) Czel, Content Manager, for coordinating all of the components of the book as it was being produced.
- Lori Hazzard, Senior Project Manager of MPS Limited, for taking care of the amazing number of details involved in turning my manuscript into a book. Thank you, Lori, not only for taking care of details, but for your flexibility and your willingness to take care of all of those "special requests" that I made during the production process.
- Bethany Bourgeois, for the striking cover.
- Heather Mann, for her expert and creative copyediting.

In addition to the help received from people on the editorial and production side, Laura and I also received a great deal of help from perception researchers. One of the things I have learned in my years of writing is that other people's advice is crucial. The field of perception is a broad one, and we have relied heavily on the advice of experts in specific areas to alert us to emerging new research and to check the content for accuracy. The following is a list of "expert reviewers," who checked the relevant chapter from the 10th edition for accuracy and completeness, and provided suggestions for updating.

Chapter 5

Joseph Brooks
Keele University

Chapter 6

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Simon-Fraser University

Chapter 7

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Chapter 9

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Chapter 13
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Chapter 14
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University of Toronto

Howard Nussbaum
University of Chicago

Chapter 15
Sliman Bensmaia
University of Chicago

Tor Wager
Dartmouth College

Chapter 16
Donald Wilson
New York University

I also thank the following people who donated photographs and research records for illustrations that are new to this edition.

Sliman Bensmaia
University of Chicago

Jack Gallant
University of California, Berkeley

Daniel Kish
Visoneers.org

Jenny Reed
University of Newcastle

István Winkler
University of Helsinki

Chen Yu
Indiana University

A Note on the Writing of This Edition

Taking the 10th edition as our starting point, this edition was created by myself (B. G.) and Laura Cacciamani. Laura revised Chapters 1–5, and is therefore responsible for the greatly improved organization of Chapters 1–4, which introduce the field of perception and which set the stage for the discussion of the different aspects of perception in the chapters that follow. I revised Chapters 6–16. We read and commented on each other's chapters and made suggestions regarding both the writing and the content, so this was, in a very real sense, a collaborative project.

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ELEVENTH EDITION

Sensation and Perception

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Perception is a miracle. Somehow, the markings on this page become a sidewalk, stone walls, and a quaint ivy-covered house. Even more miraculous is that if you were standing in the real scene, the flat image on the back of your eye is transformed into three-dimensional space that you can walk through. This book explains how this miracle happens.

Bruce Goldstein

Learning Objectives

After studying this chapter, you will be able to …

- Explain the seven steps of the perceptual process.
- Differentiate between "top-down" and "bottom-up" processing.
- Describe how knowledge can influence perception.
- Understand how perception can be studied by determining the relationships between stimulus and behavior, stimulus and physiology, and physiology and behavior.
- Explain "absolute threshold" and "difference threshold" and the various methods that can be used to measure them.
- Describe how perception above threshold can be measured by considering five questions about the perceptual world.
- Understand the importance of the distinction between physical stimuli and perceptual responses.

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CHAPTER 1

Introduction to Perception

CHAPTER CONTENTS

1.1 Why Read This Book?

1.2 Why Is This Book Titled *Sensation and Perception?*

1.3 The Perceptual Process

Distal and Proximal Stimuli (Steps 1 and 2)

Receptor Processes (Step 3)

Neural Processing (Step 4)

Behavioral Responses (Steps 5–7)

Knowledge

DEMONSTRATION: Perceiving a Picture

1.4 Studying the Perceptual Process

The Stimulus–Behavior Relationship (A)

The Stimulus–Physiology Relationship (B)

The Physiology–Behavior Relationship (C)

TEST YOURSELF 1.1

1.5 Measuring Perception

Measuring Thresholds

METHOD: Determining the Threshold

Measuring Perception Above Threshold

METHOD: Magnitude Estimation

SOMETHING TO CONSIDER: Why Is the Difference Between Physical and Perceptual Important?

TEST YOURSELF 1.2

THINK ABOUT IT

Some Questions We Will Consider:

- Why should you read this book? (p. 5)
- What is the sequence of steps from looking at a stimulus like a tree to perceiving the tree? (p. 6)
- What is the difference between perceiving something and recognizing it? (p. 9)
- How do perceptual psychologists go about measuring the varied ways that we perceive the environment? (p. 11)

In July of 1958, the *New York Times* published an intriguing article entitled, "Electronic 'Brain' Teaches Itself." The article described a new, potentially revolutionary technological advancement: "... an electronic computer named the Perceptron which, when completed in about a year, is expected to be the first non-living mechanism able to perceive, recognize, and identify its surroundings without human training or control."

The first Perceptron, created by psychologist Frank Rosenblatt (1958), was a room-sized five-ton computer (**Figure 1.1**) that could teach itself to distinguish between basic images, such as cards with markings on the left versus on the right. Rosenblatt claimed that this device could "... learn to recognize similarities or identities between patterns of optical, electrical, or tonal information, in a manner which may be closely analogous to the perceptual processes of a biological brain" (Rosenblatt, 1957). A truly astounding claim! And, in fact, Rosenblatt and other computer scientists in the 1950s and 1960s proposed that it would take only about a decade or so to create a "perceiving machine," like the Perceptron, that could understand and navigate the environment with humanlike ease.

So how did Rosenblatt's Perceptron do in its attempt to duplicate human perception? Not very well, since it took 50 trials to learn the simple task of telling whether a card had a mark on the left or on the right, and it was unable to carry out more complex tasks. It turns out that perception is much more complex than Rosenblatt or his Perceptron could comprehend. This invention therefore received mixed feedback from the field, and ultimately this line of research was dropped for many years. However, Rosenblatt's idea that a computer could be trained to learn perceptual patterns laid the groundwork for a resurgence of interest in this area in the 1980s, and many now consider Rosenblatt's work to be a key precursor to modern artificial intelligence (Mitchell, 2019; Perez et al., 2017).

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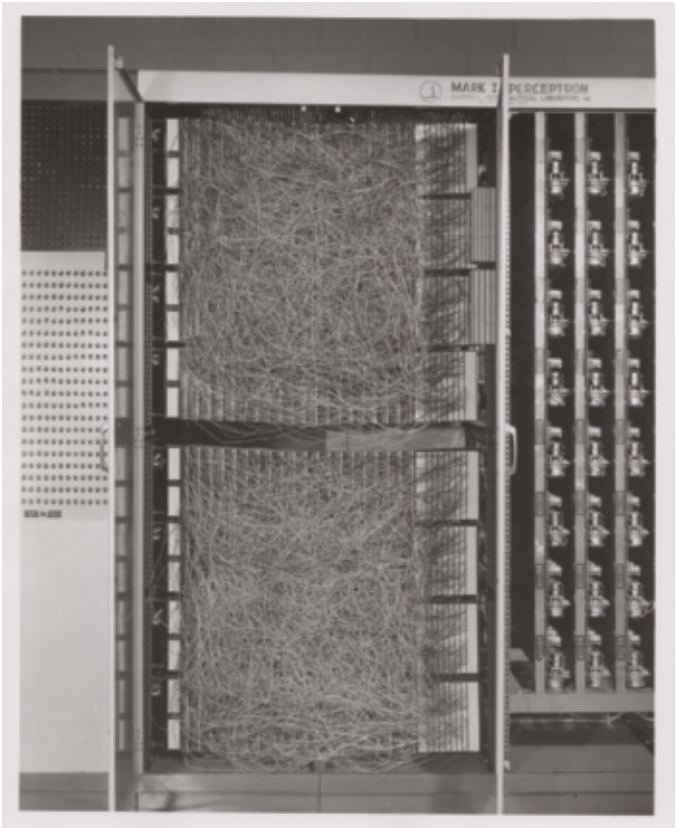

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Figure 1.1 Frank Rosenblatt's original "Perceptron" machine.

Now over 60 years later, although great strides have been made in computer vision, computers still can't perceive as well as humans (Liu et al., 2019). Consider **Figure 1.2**, which shows pictures similar to those that were provided to a computer, which then created descriptions for each image (Fei-Fei, 2015). For example, the computer identified a scene similar to the one in **Figure 1.2a** as "a large plane sitting on a runway." But mistakes occur, as when a picture similar to the one in **Figure 1.2b** was identified as "a young boy holding a baseball bat." The computer's problem is that it doesn't have the huge storehouse of information that humans begin accumulating as soon as they are born. If a computer has never seen a toothbrush, it identifies it as something with a similar shape. And, although the computer's response to the airplane picture is accurate, it is beyond the computer's capabilities to recognize that this is a picture of airplanes on display, perhaps at an air show, and that the people are not passengers but are visiting the air show. So on one hand, we have come a very long way from the first attempts in the 1950s to design computer-vision systems, but to date, humans still out-perceive computers.

Why did early computer scientists think they would be able to create a computer capable of human-like perception within a decade or so, when it has actually taken over 60 years, and we still aren't there yet? One answer to this question is that **perception**—the experiences that result from stimulation of the senses—is something we usually accomplish so easily that we often don't even give it a second thought. Perception seems to "just happen." We open our eyes and see a landscape, a campus building, or a group of people. But the reality, as you will appreciate after reading this book, is that the mechanisms responsible for perception are extremely complex.

Throughout this book, we'll see many more examples illustrating how complex and amazing perception is. Our goal is to understand how humans and animals perceive, starting with the detectors—located in the eyes, ears, skin, tongue, nose, and mouth—and then moving on to the "computer"—the brain. We want to understand how we sense things in the environment and interact with them.

In this chapter, we will consider some practical reasons for studying perception, how perception occurs in a sequence of steps, and how perception can be measured.

(a)

(b)

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Figure 1.2 Pictures similar to one that a computer vision program identified as (a) "a large plane sitting on a runway" and (b) "a young boy holding a baseball bat." (Adapted from Fei-Fei, 2015)

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1.1 Why Read This Book?

The most obvious answer to the question "Why read this book?" is that it is required reading for a course you are taking. Thus, it is probably an important thing to do if you want to get a good grade. But beyond that, there are a number of other reasons for reading this book. For one thing, it will provide you with information that may be helpful in other courses and perhaps even your future career. If you plan to go to graduate school to become a researcher or teacher in perception or a related area, this book will provide you with a solid background to build on. In fact, many of the research studies you will read about were carried out by researchers who read earlier editions of this book when they were undergraduates.

The material in this book is also relevant to future studies in medicine or related fields, because much of our discussion is about how the body operates. Medical applications that depend on an understanding of perception include devices to restore perception to people who have lost vision or hearing and treatments for pain. Other applications include autonomous vehicles that can find their way through unfamiliar environments, face recognition systems that can identify people as they pass through airport security, speech recognition systems that can understand what someone is saying, and highway signs that are visible to drivers under a variety of conditions.

But reasons to study perception extend beyond the possibility of creating or understanding useful applications. Studying perception can help you become more aware of the nature of your own perceptual experiences. Many of the everyday experiences that you take for granted—such as tasting food, looking at a painting in a museum, or listening to someone talking—can be appreciated at a deeper level by considering questions such as "Why do I lose my sense of taste when I have a cold?" "How do artists create an impression of depth in a picture?" and "Why does an unfamiliar language sound as if it is one continuous stream of sound, without breaks between words?" This book will not only answer these questions but will answer other questions that you may not have thought of, such as "Why don't I see colors at dusk?" and "How come the scene around me doesn't appear to move as I walk through it?" Thus, even if you aren't planning to become a physician or an autonomous vehicle designer, you will come away from reading this book with a heightened appreciation of both the complexity and the beauty of the mechanisms responsible for your perceptual experiences, and perhaps even with an enhanced awareness of the world around you.

Because perception is something you experience constantly, knowing about how it works is interesting in its own right. To appreciate why, consider what you are experiencing right now. If you touch the page of this book, or look out at what's around you, you might get the feeling that you are perceiving exactly what is "out there" in the environment. After all, touching this page puts you in direct contact with it, and it seems likely that what you are seeing is what is actually there. But one of the things you will learn as you study perception is that everything you see, hear, taste, feel, or smell is the result of the activity in your nervous system and your knowledge gained from past experience.

Think about what this means. There are things out there that you want to see, hear, taste, smell, and feel. But the only way to achieve this is by activating *sensory receptors* in your body designed to respond to light energy, sound energy, chemical stimuli, and pressure on the skin. When you run your fingers over the pages of this book, you feel the page and its texture because the pressure and movement are activating small receptors just below the skin. Thus, whatever you are feeling depends on the activation of these receptors. If the receptors weren't there, you would feel nothing, or if they had different properties, you might feel something different from what you feel now. This idea that *perception depends on the properties of the sensory receptors* is one of the themes of this book.

A few years ago, I received an email from a student (not one of my own, but from another university) who was using an earlier edition of this book.[1] In her email, "Jenny" made a number of comments about the book, but the one that struck me as being particularly relevant to the question "Why read this book?" is the following: "By reading your book, I got to know the fascinating processes that take place every second in my brain, that are doing things I don't even think about." Your reasons for reading this book may turn out to be totally different from Jenny's, but hopefully you will find out some things that will be useful, or fascinating, or both.

1.2 Why Is This Book Titled *Sensation and Perception*?

You may have noticed that so far in our discussion we've used the word *perception* quite a lot, but haven't mentioned *sensation*, even though the title of this book is *Sensation and Perception*. Why has *sensation* been ignored? To answer this question, let's consider the terms *sensation* and *perception*. When a distinction is made between *sensation* and *perception*, **sensation** is often identified as involving simple "elementary" processes that occur right at the beginning of a sensory system, such as when light reaches the eye, sound waves enter the ear, or your food touches your tongue. In contrast, *perception* is identified with complex processes that involve higher-order mechanisms such as interpretation and memory that involve activity in the brain—for instance, identifying the food you're eating

[1]Who is "I"? In various places in the book you will see first-person references such as this one ("*I* received an email") or others, like "a student in *my* class," or "*I* tell my students," or "*I* had an interesting experience." Because this book has two authors, you may wonder who *I* or *my* is. The answer is that, unless otherwise noted, it is author B. G., because most of the first-person references in this edition are carried over from the 10th edition.

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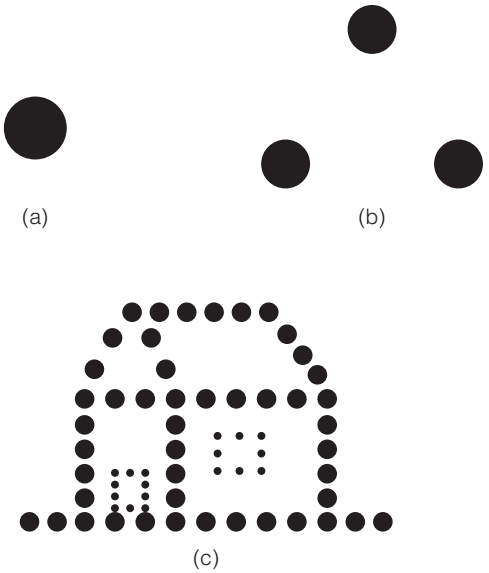

Figure 1.3 (a) One dot, (b) a triangle, (c) a house. What do these stimuli tell us about sensations and perceptions? See text for discussion.

and remembering the last time you had it. It is therefore often stated, especially in introductory psychology textbooks, that *sensation* involves detecting elementary properties of a stimulus (Carlson, 2010), and perception involves the higher brain functions involved in interpreting events and objects (Myers, 2004).

Keeping this distinction in mind, let's consider an example from the sense of vision in **Figure 1.3. Figure 1.3a** is extremely simple—a single dot. Let's for the moment assume that this simplicity means that there is no interpretation or higher-order processes, so sensation is involved. Looking at **Figure 1.3b**, with three dots, we might now think that we are dealing with perception, because we interpret the three dots as creating a triangle. Going even further, we can say that **Figure 1.3c**, which is made up of many dots, is a "house." Surely this must be perception because it involves many dots and our past experience with houses. But let's return to Figure 1.3a, which we called a dot. As it turns out, even a stimulus this simple can be seen in more than one way. Is this a black dot on a white background or a hole in a piece of white paper? Now that interpretation is involved, does our experience with Figure 1.3a become *perception*?

This example illustrates that deciding what is *sensation* and what is *perception* is not always obvious, or even that useful. As we will see in this book, there are experiences that depend heavily on processes that occur right at the beginning of a sensory system, in the sensory receptors or nearby, and there are other experiences that depend on interpretation and past experiences, using information stored in the brain. But this book takes the position that calling some processes *sensation* and others *perception* doesn't add anything to our understanding of how our sensory experiences are created, so the term *perception* is used almost exclusively throughout this book.

Perhaps the main reason not to use the term *sensation* is that, with the exception of papers on the history of perception research (Gilchrist, 2012), the term *sensation* appears only rarely in modern research papers (mainly in papers on the sense of taste, which refer to taste sensations, and touch which refer to touch sensations), whereas the term *perception* is extremely common. Despite the fact that introductory psychology books may distinguish between sensation and perception, most perception researchers don't make this distinction.

So why is this book called *Sensation and Perception*? Blame history. Sensation was discussed in the early history of perceptual psychology, and courses and textbooks followed suit by including *sensation* in their titles. But while researchers eventually stopped using the term *sensation*, the titles of the courses and books remained the same. So sensations are historically important (we will discuss this briefly in Chapter 5), but as far as we are concerned, everything that involves understanding how we experience the world through our senses comes under the heading of perception. With that bit of terminology out of the way, we are now ready to describe perception as involving a number of steps, which we will call the perceptual process. These steps begin with a stimulus in the environment and end with perceiving the stimulus, recognizing it, and taking action relative to it.

1.3 The Perceptual Process

Perception happens at the end of what can be described, with apologies to the Beatles, as a long and winding road (McCartney, 1970). This road begins outside of you, with stimuli in the environment—trees, buildings, birds chirping, smells in the air—and ends with the behavioral responses of perceiving, recognizing, and taking action. We picture this journey from stimuli to responses by the seven steps in **Figure 1.4**, called the perceptual process. The process begins with a stimulus in the environment (a tree in this example) and ends with the conscious experiences of perceiving the tree, recognizing the tree, and taking action with respect to the tree (like walking up to take a closer look).

Although this example of perceiving a tree is from the sense of vision, keep in mind as we go through these steps that the same general process applies to the other senses as well. Furthermore, because this process is involved in everything we will be describing in this book, it is important to note that Figure 1.4 is a simplified version of what happens. First, many things happen within each "box." For example, "neural processing" involves understanding not only how cells called neurons work, but how they interact with each other and how they operate within different areas of the brain. Another reason we say that our process is simplified is that steps in the perceptual process do not always unfold in a one-follows-the-other order. For example, research has shown that perception ("I see something") and recognition ("That's a tree") may not always happen one after another, but could happen at the same time, or even in reverse order (Gibson & Peterson, 1994; Peterson, 2019). And when perception or recognition leads to action ("Let's have a closer look at the tree"), that action could change perception and recognition ("Looking closer shows that what I thought was an oak tree turns out to be a maple tree"). This is why there are bidirectional arrows between perception, recognition, and action. In addition, there is an arrow from "action"

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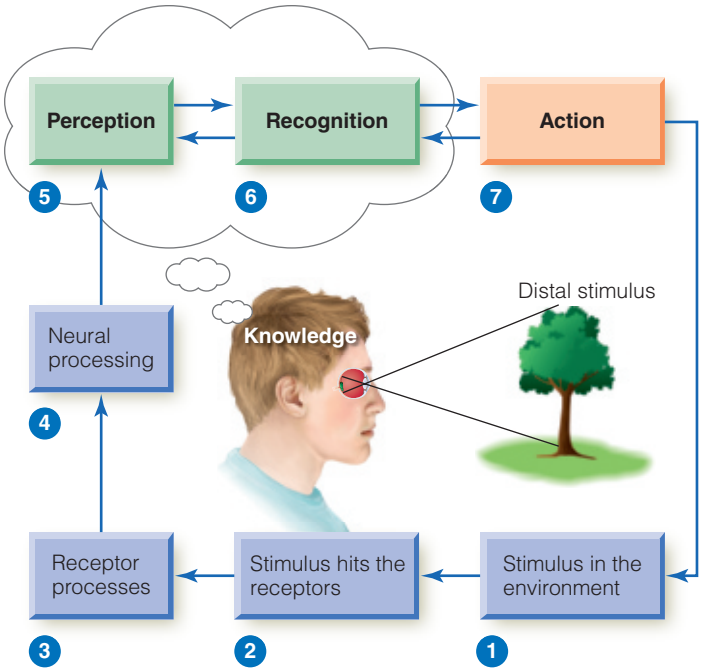

Figure 1.4 The perceptual process. These seven steps, plus "knowledge" inside the person's brain, summarize the major events that occur between the time a person looks at the stimulus in the environment (the tree in this example) and perceives the tree, recognizes it, and takes action toward it. Information about the stimulus in the environment (the *distal stimulus*; Step 1) hits the receptors, resulting in the *proximal stimulus* (Step 2), which is a representation of the stimulus on the retina. *Receptor processes* (Step 3) include transduction and the shaping of perception by the properties of the receptors. *Neural processing* (Step 4) involves interactions between the electrical signals traveling in networks of neurons. Finally, the behavioral responses—*perception*, *recognition*, and *action*—are generated (Steps 5–7).

back to the stimulus. This turns the perceptual process into a "cycle" in which taking action—for example, walking toward the tree—changes the observer's view of the tree.

Even though the process is simplified and only depicts the perceptual process in one sense, Figure 1.4 provides a good way to think about how perception occurs and introduces some important principles that will guide our discussion of perception throughout this book. In the first part of this chapter, we will briefly describe each stage of the process; in the second part, we will consider ways of measuring the relationship between stimuli and perception.

Distal and Proximal Stimuli (Steps 1 and 2)

There are stimuli within the body that produce internal pain and enable us to sense the positions of our body and limbs. But for the purposes of this discussion, we will focus on stimuli that exist "out there" in the environment, like a tree in the woods that you can see, hear, smell, and feel (and taste, if you wanted to be adventurous). Using this example, we will consider what happens in the first two steps of the perceptual process in which stimuli from the environment reach the sensory receptors.

We begin with the tree that the person is observing, which we call the **distal stimulus** (Step 1). It is called distal because it is "distant"—out there in the environment. The person's perception of the tree is based not on the tree getting into his eye or ear (ouch!), but on light reflected from the tree entering the eye and reaching the visual receptors, and the pressure changes in the air caused by the rustling leaves entering the ear and reaching the auditory receptors. This representation of the tree on the receptors is the **proximal stimulus** (Step 2), so called because it is "in proximity" to the receptors.

The light and pressure waves that stimulate the receptors introduce one of the central principles of perception, the **principle of transformation**, which states that *stimuli and responses created by stimuli are transformed, or changed, between the distal stimulus and perception*.

For example, the first transformation occurs when light hits the tree and is then reflected from the tree to the person's eyes. The nature of the reflected light depends on properties of the light energy hitting the tree (is it the midday sun, light on an overcast day, or a spotlight illuminating the tree from below?), properties of the tree (its textures, shape, the fraction of light hitting it that it reflects), and properties of the atmosphere through which the light is transmitted (is the air clear, dusty, or foggy?). As this reflected light enters the eye, it is transformed again as it is focused by the eye's optical system (discussed further in Chapter 3) onto the retina, a 0.4-mm-thick network of nerve cells which contains the receptors for vision.

The fact that an image of the tree is focused on the receptors introduces another principle of perception, the **principle of representation**, which states that *everything a person perceives is based not on direct contact with stimuli but on representations of stimuli that are formed on the receptors and the resulting activity in the person's nervous system.*

The distinction between the distal stimulus (Step 1) and the proximal stimulus (Step 2) illustrates both transformation and representation. The distal stimulus (the tree) is *transformed* into the proximal stimulus, and this image *represents* the tree in the person's eyes. But this transformation from "tree" to "image of the tree on the receptors" is just the first in a series of transformations. We're only on Step 2 of the perceptual process, and we can already begin to understand the complexity of perception in these transformations! The next transformation occurs within the receptors themselves.

Receptor Processes (Step 3)

Sensory receptors are cells specialized to respond to environmental energy, with each sensory system's receptors specialized to respond to a specific type of energy. **Figure 1.5** shows examples of receptors from each of the senses. Visual receptors respond to light, auditory receptors to pressure changes in the air, touch receptors to pressure transmitted through the skin, and smell and taste receptors to chemicals entering the nose and mouth. When the sensory receptors receive the information from the environment, such as light reflected from the tree, they do two things: (1) They transform environmental

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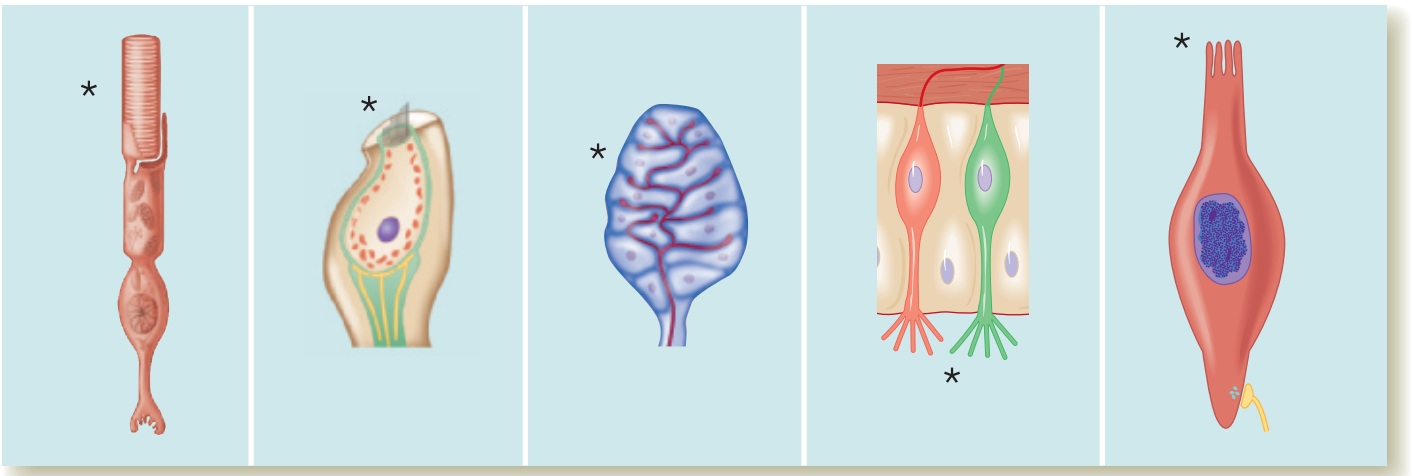

Figure 1.5 Receptors for (a) vision, (b) hearing, (c) touch, (d) smell, and (e) taste. Each of these receptors is specialized to transduce a specific type of environmental energy into electricity. Stars indicate the place on the receptor neuron where the stimulus acts to begin the process of transduction.

energy into electrical energy; and (2) they shape perception by the way they respond to different properties of the stimuli.

The transformation of environmental energy (such as light, sound, or thermal energy) to electrical energy is called **transduction**. For example, if you were to run your fingers over the bark of the tree, the stimulation of pressure receptors in your fingers would cause these receptors to produce electrical signals representing the texture of the bark. By transforming environmental energy into electrical energy, your sensory receptors are allowing the information that is "out there," like the texture of the tree, to be transformed into a form that can be understood by your brain. Transduction by the sensory receptors is, therefore, crucial for perception. Another way to think about transduction is that your sensory receptors are like a bridge between the external sensory world and your internal (neural) representation of that world. In the next step of the perceptual process, further processing of that neural representation takes place.

Neural Processing (Step 4)

Once transduction occurs, the tree becomes represented by electrical signals in thousands of sensory receptors (visual receptors if you're looking at the tree, auditory receptors if you're hearing the leaves rustling, and so on). But what happens to these signals? As we will see in Chapter 2, they travel through a vast interconnected network of neurons that (1) *transmit* signals from the receptors to the brain and then within the brain; and (2) *change* (or *process*) these signals as they are transmitted. These changes occur because of interactions between neurons as the signals travel from the receptors to the brain. Because of this processing, some signals become reduced or are prevented from getting through, and others are amplified so they arrive at the brain with added strength. This processing then continues as signals travel to various places in the brain.

The changes in these signals that occur as they are transmitted through this maze of neurons is called **neural processing**. This processing will be discussed in much more detail in later chapters as we describe each sense individually. However, there are commonalities in neural processing between the senses.

For instance, the electrical signals created through transduction are often sent to a sense's **primary receiving area** in the cerebral cortex of the brain, as shown in **Figure 1.6**. The **cerebral cortex** is a 2-mm-thick layer that contains the machinery for creating perceptions, as well as other functions, such as language, memory, emotions, and thinking. The primary receiving area for vision occupies most of the **occipital lobe**; the area for hearing is located in part of the **temporal lobe**; and the area for the skin senses—touch, temperature, and pain—is located in an area in the **parietal lobe**. As we study each sense in detail, we will see that once signals reach the primary receiving areas, they are then transmitted

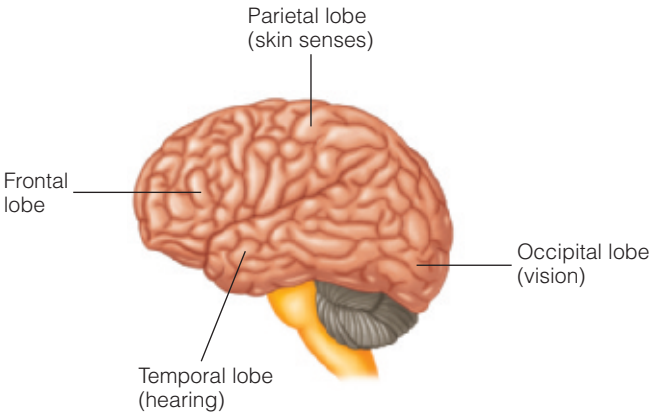

Figure 1.6 The four lobes of the brain, with the primary receiving areas for vision, hearing, and the skin senses (touch, temperature, and pain) indicated.

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Figure 1.7 The behavioral responses of the perceptual process: *perception*, *recognition*, and *action*.

to many other structures in the brain. For example, the frontal lobe receives signals from all of the senses, and it plays an important role in perceptions that involve the coordination of information received through two or more senses.

The sequence of transformations that occurs between the receptors and the brain, and then within the brain, means that the pattern of electrical signals in the brain is changed compared to the electrical signals that left the receptors. It is important to note, however, that although these signals have changed, they still represent the tree. In fact, the changes that occur as the signals are transmitted and processed are crucial for achieving the next step in the perceptual process, the *behavioral responses*.

Behavioral Responses (Steps 5–7)

Finally, after all of that transformation, transduction, transmission, and processing, we reach the behavioral responses (**Figure 1.7**). This transformation is perhaps the most miraculous of all, because electrical signals have been transformed into the *conscious experience* of perception (Step 5), which then leads to *recognition* (Step 6). We can distinguish between *perception*, which is conscious awareness of the tree, and recognition, which is placing an object in a category, such as "tree," that gives it meaning, by considering the case of Dr. P., a patient described by neurologist Oliver Sacks (1985) in the title story of his book *The Man Who Mistook His Wife for a Hat.*

Dr. P., a well-known musician and music teacher, first noticed a problem when he began having trouble recognizing his students visually, although he could immediately identify them by the sound of their voices. But when Dr. P. began misperceiving common objects, for example addressing a parking meter as if it were a person or expecting a carved knob on a piece of furniture to engage him in conversation, it became clear that his problem was more serious than just a little forgetfulness. Was he blind, or perhaps crazy? It was clear from an eye examination that he could see well, and by many other criteria it was obvious that he was not crazy.

Dr. P.'s problem was eventually diagnosed as visual form agnosia—an inability to recognize objects—that was caused by a brain tumor. He perceived the parts of objects but couldn't identify the whole object, so when Sacks showed him a glove, as in **Figure 1.8**, Dr. P. described it as "a continuous surface unfolded on itself. It appears to have five outpouchings, if this is the word." When Sacks asked him what it was, Dr. P. hypothesized that it was "a container of some sort. It could be a change purse, for example, for coins of five sizes." The normally easy process of object recognition had, for Dr. P., been derailed by his brain tumor. He could perceive the object and recognize parts of it, but he couldn't perceptually assemble the parts in a way that would enable him to recognize the object as a whole. Cases such as this show that it is important to distinguish between perception and recognition.

The final behavioral response is action (Step 7), which involves motor activities in response to the stimulus. For example, after having perceived and recognized the tree, the person might decide to walk toward the tree, touch the tree, have a picnic under it, or climb it. Even if he doesn't decide to interact directly with the tree, he is taking action when he moves his eyes and head to look at different parts of the tree, even if he is standing in one place.

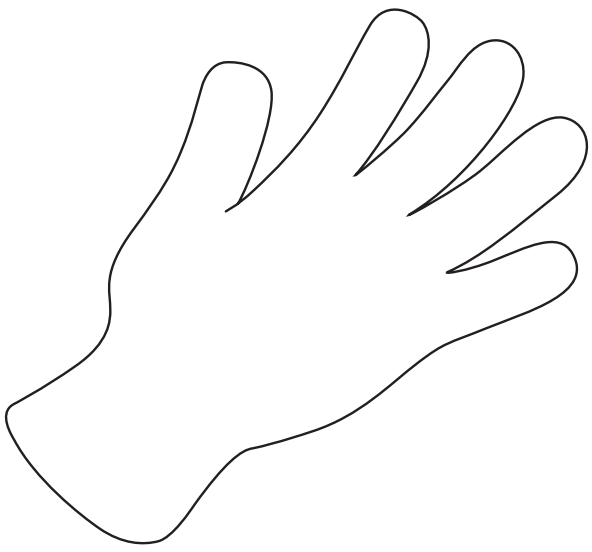

Figure 1.8 How Dr. P.—a patient with visual form agnosia—responded when his neurologist showed him a glove and asked him what it was.

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Some researchers see action as an important outcome of the perceptual process because of its importance for survival. David Milner and Melvyn Goodale (1995) propose that early in the evolution of animals, the major goal of visual processing was not to create a conscious perception or "picture" of the environment but to help the animal control navigation, catch prey, avoid obstacles, and detect predators—all crucial functions for the animal's survival.

The fact that perception often leads to action—whether it be an animal's increasing its vigilance when it hears a twig snap in the forest or a person's deciding to interact with an object or just look more closely at something that looks interesting—means that perception is a continuously changing process. For example, the visual and auditory representations of the tree change every time the person moves his body relative to the tree, as the tree might look and sound different from different angles, and this change creates new representations and a new series of transformations. Thus, although we can describe the perceptual process as a series of steps that "begins" with the distal stimulus and "ends" with perception, recognition, and action, the overall process is dynamic and continually changing.

Knowledge

Our diagram of the perceptual process includes one more factor: *knowledge*. **Knowledge** is any information that the perceiver brings to a situation, such as prior experience or expectations. Knowledge is placed inside the person's brain in Figure 1.4 because it can affect a number of the steps in the perceptual process. Knowledge that a person brings to a situation can be information acquired years ago or, as in the following demonstration, information just recently acquired.

DEMONSTRATION | Perceiving a Picture

After looking at the drawing in **Figure 1.9**, close your eyes, turn to page 12, and open and shut your eyes rapidly to briefly expose the picture in **Figure 1.13**. Decide what the second picture is; then open your eyes and read the explanation below it. Do this now, before reading further.

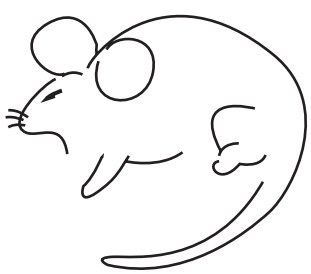

Figure 1.9 See above. (Adapted from Bugelski & Alampay, 1961)

Did you identify Figure 1.13 as a rat (or a mouse)? If you did, you were influenced by the clearly rat- or mouselike figure you observed initially. But people who first observe **Figure 1.16** instead of Figure 1.9 usually identify Figure 1.13 as a man. (Try this on someone else.) This demonstration, which is called the **rat–man demonstration**, shows how recently acquired knowledge ("that pattern is a rat") can influence perception.

An example of how knowledge acquired years ago can influence the perceptual process is your ability to **categorize**—to place objects into categories. This is something you do every time you name an object. "Tree," "bird," "branch," "car," and everything else you can name are examples of objects being placed into categories that you learned as a young child and that have become part of your knowledge base.

Another way to describe the effect of information that the perceiver brings to the situation is by distinguishing between bottom-up processing and top-down processing. **Bottom-up processing** (also called **data-based processing**) is processing that is based on the stimuli reaching the receptors. These stimuli provide the starting point for perception because, with the exception of unusual situations such as drug-induced perceptions or "seeing stars" from a bump to the head, perception involves activation of the receptors. The woman sees the moth on the tree in **Figure 1.10** because of processes triggered by the moth's image on her visual receptors. The image is the "incoming data" that is the basis of bottom-up processing.

Top-down processing (also called **knowledge-based processing**) refers to processing that is based on knowledge. When the woman in Figure 1.10 labels what she is seeing as a "moth" or perhaps a particular kind of moth, she is accessing what she has learned about moths from prior experience. Knowledge such as this isn't always involved in perception, but as we will see, it often is—sometimes without our even being aware of it.

To experience top-down processing in action, try reading the following sentence:

M*RY H*D * L*TTL* L*MB

If you were able to do this, even though all of the vowels have been omitted, you probably used your knowledge of English words, how words are strung together to form sentences, and your familiarity with the nursery rhyme to create the sentence (Denes & Pinson, 1993).

Students often ask whether top-down processing is always involved in perception. The answer to this question is that it is "very often" involved. There are some situations, typically involving very simple stimuli, in which top-down processing may not be involved. For example, perceiving a single flash of easily visible light is probably not affected by a person's prior experience. However, as stimuli become more complex, the role of top-down processing increases. In fact, a person's past experience is usually involved in perception of real-world scenes, even though in most cases the person is unaware of this influence. One of the themes of this book is that our knowledge of how things usually appear in the environment, based on our past experiences, can play an important role in determining what we perceive.

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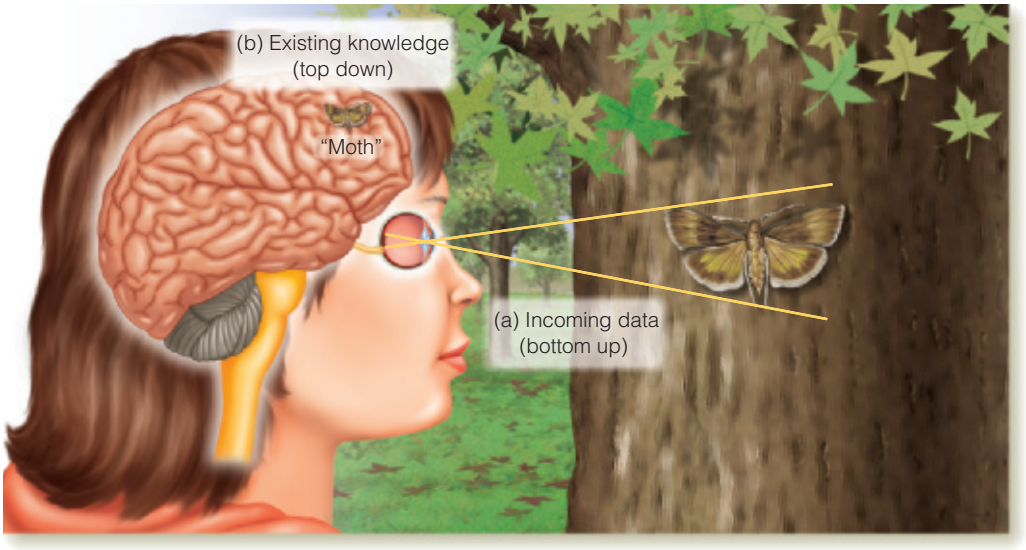

Figure 1.10 Perception is determined by an interaction between bottom-up processing, which starts with the image on the receptors, and top-down processing, which brings the observer's knowledge into play. In this example, (a) the image of the moth on the woman's visual receptors initiates bottom-up processing; and (b) her prior knowledge of moths contributes to top-down processing.

1.4 Studying the Perceptual Process

To better understand how the perceptual process is studied, we can simplify it from seven steps (Figure 1.4) into three major components (**Figure 1.11**):

- Stimulus (distal and proximal; Steps 1–2)
- Physiology (receptors and neural processing; Steps 3–4)
- Behavior (perception, recognition, action; Steps 5–7)

The goal of perceptual research is to understand the relationships indicated by arrows A, B, and C between these three components. For example, some research studies examine how we get from a stimulus to behavior (arrow A), such as the pressure of someone touching your shoulder (the stimulus) and feeling the touch and reacting to it (the behavior). Other studies have investigated how a given stimulus affects physiology (arrow B), such as how the pressure on your shoulder leads to neural firing. And still other work addresses the relationship between physiology and behavior (arrow C), such as how neural firing results in the feeling on your shoulder.

In the following sections, we use a visual phenomenon called the oblique effect to show how each of these relationships can be studied to understand the perceptual process. The **oblique effect** is that people see vertical or horizontal lines better than lines oriented obliquely (at any orientation other than vertical or horizontal). We begin by considering how the oblique effect has been studied in the context of the stimulus–behavior relationship.

The Stimulus–Behavior Relationship (A)

The **stimulus–behavior relationship** relates stimuli (Steps 1 and 2 in Figure 1.4) to behavioral responses, such as perception, recognition, and action (Steps 5–7). This was the main relationship measured during the first 100 years of the scientific study of perception, before physiological methods became widely available, and it is still being studied today.

One way to study the stimulus–behavior relationship is using an approach called **psychophysics**, which measures the relationships between the physical (the stimulus) and the psychological (the behavioral response). We will discuss various psychophysical methods in more detail later in this chapter. For now, let's consider psychophysics using the example of the oblique effect.

The oblique effect has been demonstrated by presenting black and white striped stimuli called gratings, and measuring **grating acuity**, the smallest width of lines that participants can

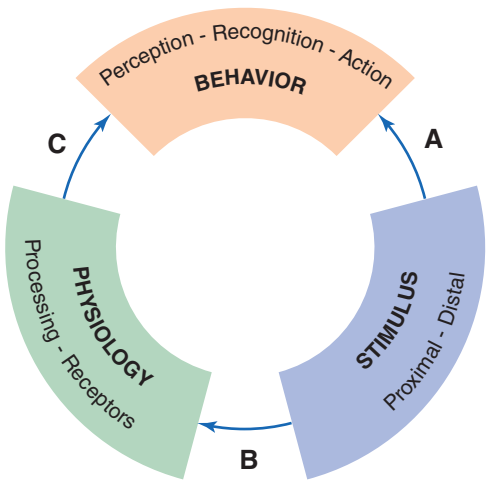

Figure 1.11 Simplified perceptual process showing the three relationships described in the text. The three boxes represent the three major components of the seven-step perceptual process: Stimulus (Steps 1 and 2); Physiology (Steps 3 and 4); and the three Behavioral responses (Steps 5–7). The three relationships that are usually measured to study the perceptual process are (A) the stimulus–behavior relationship; (B) the stimulus–physiology relationship; and (C) the physiology–behavior relationship.

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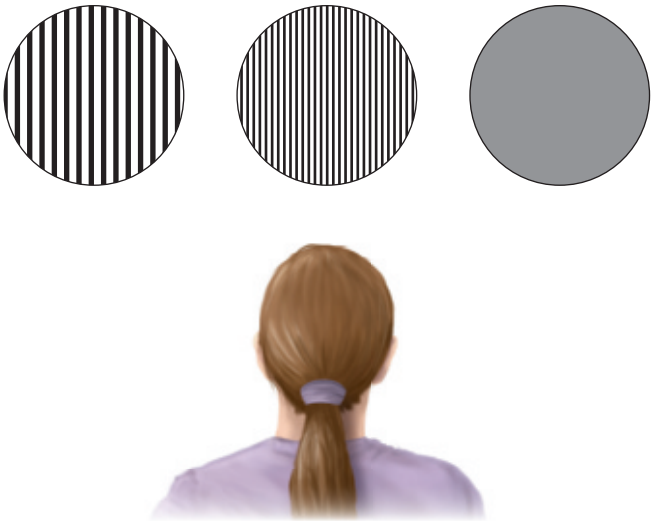

Figure 1.12 Measuring grating acuity. The finest line width at which a participant can perceive the bars in a black-and-white grating stimulus is that participant's grating acuity. Stimuli with different line widths are presented one at a time, and the participant indicates the grating's orientation until the lines are so close together that the participant can no longer indicate the orientation.

detect. One way to measure grating acuity is to ask participants to indicate the grating's orientation and testing with thinner and thinner lines (**Figure 1.12**). Eventually, the lines are so thin that they can't be seen, and the area inside the circle looks uniform, so participants can no longer indicate the grating's orientation. The smallest line-width at which the participant can still indicate the correct orientation is the grating acuity. When grating acuity is assessed at different orientations, the results show that acuity is best for gratings oriented vertically or horizontally, rather than obliquely (Appelle, 1972). This simple psychophysics experiment demonstrates a relation between the stimulus and behavior; in this case, the stimulus is oriented gratings, and the behavioral response is detecting the grating's orientation.

The Stimulus–Physiology Relationship (B)

The second stimulus relationship (Arrow B in Figure 1.11) is the **stimulus–physiology relationship**, the relationship between stimuli (Steps 1–2) and physiological responses, like neurons firing (Steps 3–4). This relationship is often studied by measuring brain activity (discussed further in Chapter 2). For example, David Coppola and coworkers (1998) measured the oblique effect physiologically by presenting lines with different orientations (**Figure 1.14a**) to ferrets. When they measured the ferret's brain activity using a technique called *optical brain imaging*, they found that horizontal and vertical orientations caused larger brain responses in visual brain areas than oblique orientations (**Figure 1.14b**).[2] This demonstrates how the oblique effect has been studied in the context of the stimulus–physiology relationship.

Note that even though the stimulus–behavior experiment was carried out on humans and the stimulus–physiology experiment was carried out on ferrets, the results are similar. Horizontal and vertical orientations result in better acuity (behavioral response) and more brain activation (physiological response) than oblique orientations. When behavioral and physiological responses to stimuli are similar like this, researchers often infer the relationship between physiology and behavior (Arrow C in Figure 1.11), which in this case would be the association between greater physiological responses to horizontals and verticals and better perception of horizontals and verticals. But in some cases, instead of just inferring this association, researchers have measured the physiology–behavior relationship directly.

Figure 1.13 Did you see a "rat" or a "man"? Looking at the more ratlike picture in Figure 1.9 increased the chances that you would see this as a rat. But if you had first seen the man version (Figure 1.16), you would have been more likely to perceive this figure as a man. (Adapted from Bugelski & Alampay, 1961)

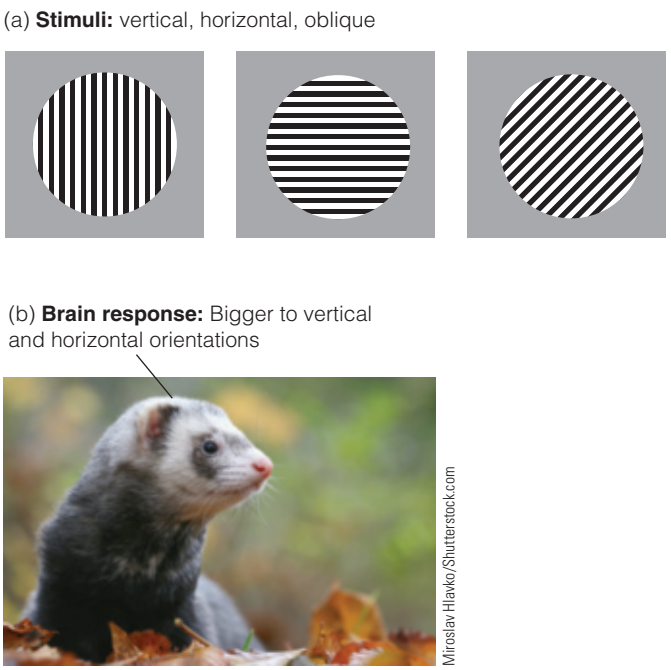
(a) **Stimuli:** vertical, horizontal, oblique
(b) **Brain response:** Bigger to vertical and horizontal orientations
Miroslav Hlavko/Shutterstock.com

Figure 1.14 Coppola and coworkers (1998) measured the relationship between bar orientation (stimuli) and brain activity (physiology) in ferrets. Verticals and horizontals generated the greatest brain activity.

[2]Because a great deal of physiological research has been done on animals, students often express concerns about how these animals are treated. All animal research in the United States follows strict guidelines for the care of animals established by organizations such as the American Psychological Association and the Society for Neuroscience. The central tenet of these guidelines is that every effort should be made to ensure that animals are not subjected to pain or distress. Research on animals has provided essential information for developing aids for people with sensory disabilities such as blindness and deafness and for helping develop techniques to ease severe pain.

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The Physiology–Behavior Relationship (C)

The physiology–behavior relationship relates physiological responses (Steps 3–4 in Figure 1.4) and behavioral responses (Steps 5–7; Arrow C in Figure 1.11). Christopher Furmanski and Stephen Engel (2000) determined the physiology–behavior relationship for different grating orientations by measuring both the brain response and behavioral sensitivity in the same participants. The behavioral measurements were made by decreasing the intensity difference between light and dark bars of a grating until the participant could no longer detect the grating's orientation. Participants were able to detect the horizontal and vertical orientations at smaller light–dark differences than for the oblique orientations. This means that participants were more sensitive to the horizontal and vertical orientations (**Figure 1.15a**). The physiological measurements were made using a technique called functional magnetic resonance imaging (fMRI), which we will describe in Chapter 2 (see page 31). These measurements showed larger brain responses to vertical and horizontal gratings than to oblique gratings (**Figure 1.15b**).

The results of this experiment, therefore, are consistent with the results of the other two oblique effect experiments that we have discussed. The beauty of this experiment is that the behavioral and physiological responses were measured in the same participants, allowing for a more direct assessment of the physiology–behavior relationship than in the previously described experiments. The reason for the visual system's preference for horizontal and vertical orientations, which has to do with the prevalence of verticals and horizontals in the environment, will be discussed in Chapter 5.

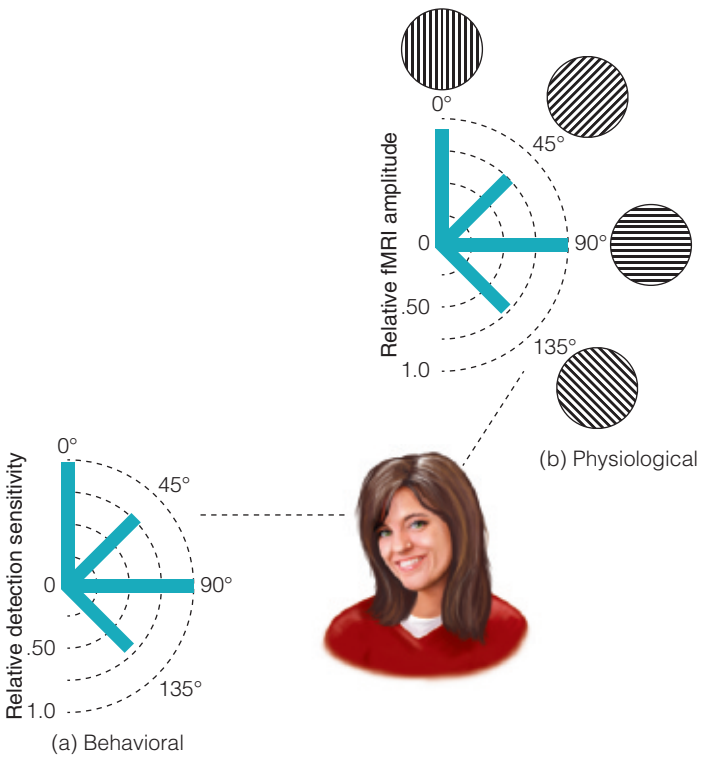

Figure 1.15 Furmanski and Engel (2000) made both behavioral and physiological measurements of participants' response to oriented gratings. (a) Bars indicate sensitivity to gratings of different orientations. Sensitivity is highest to the vertical (0 degree) and horizontal (90 degree) orientations. (b) Bars indicate fMRI amplitude to different orientations. Amplitudes were greater to the 0- and 90-degree orientations.

We have now seen how the perceptual process can be studied by investigating the relationships between its three main components: the stimulus, physiology, and behavior. One of the things that becomes apparent when we step back and look at the three relationships is that each one provides information about different aspects of the perceptual process. An important message of this book is that to truly understand perception, we have to study it by measuring both behavioral and physiological relationships. Furthermore, as discussed earlier in this chapter, it's important to consider how the knowledge, memories, and expectations that people bring to a situation can influence their perception (like in the rat–man demonstration in Figure 1.13). Only by considering both behavior and physiology together, along with potential influences of knowledge-based processing, can we create a complete picture of the mechanisms responsible for perception.

TEST YOURSELF 1.1

1. What are some reasons for studying perception?
2. Describe the process of perception as a series of seven steps, beginning with the distal stimulus and culminating in the behavioral responses of perceiving, recognizing, and acting.
3. What is the role of higher-level or knowledge-based processes in perception? Be sure you understand the difference between bottom-up and top-down processing.
4. What does it mean to say that perception can be studied by measuring three relationships? Give an example of how the oblique effect was studied by measuring each relationship.

1.5 Measuring Perception

So far we've pictured the perceptual process as having a number of steps (Figure 1.4), and we've demonstrated how we can study the process by studying three different relationships (Figure 1.11). But what, exactly, do we *measure* to determine these relationships? In this section we will describe a number of different ways to measure behavioral responses. We will describe how to measure physiological responses in Chapter 2.

What is measured in an experiment looking at the relationship between stimuli and behavior? The grating acuity experiment described on page 12 (Figure 1.12) measured the absolute threshold for seeing fine lines. The absolute threshold is the smallest stimulus level that can just be detected. In the grating acuity example, this threshold was the smallest line width that can be detected. But we can also look to the other senses for more examples. For instance, if you're making a stew and decide that you want to add salt for flavor, the absolute threshold would be

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the smallest amount of salt that you would need to add in order to just be able to taste it. For the sense of hearing, it might be the intensity of a whisper that you can just barely hear.

These examples show that **thresholds** measure the limits of sensory systems; they are measures of minimums—the smallest line-width that can be detected, the smallest concentration of a chemical we can taste or smell, the smallest amount of sound energy we can hear. Thresholds have an important place in the history of perceptual psychology, and of psychology in general, so let's consider them in more detail before describing other ways of measuring perception. As we will now see, the importance of being able to accurately measure thresholds was recognized very early in the history of the scientific study of the senses.

Measuring Thresholds

Gustav Fechner (1801–1887), professor of physics at the University of Leipzig, introduced a number of ways of measuring thresholds. Fechner had wide-ranging interests, having published papers on electricity, mathematics, color perception, aesthetics (the judgment of art and beauty), the mind, the soul, and the nature of consciousness. But of all his accomplishments, the most significant one was providing a new way to study the mind.

Let's view Fechner's thinking about the mind against the backdrop of how people thought about the mind in the mid-1800s. Prevailing thought at that time was that it was impossible to study the mind. The mind and the body were thought to be totally separate from one another. People saw the body as physical and therefore something that could be seen, measured, and studied, whereas the mind was considered not physical and was therefore invisible and something that couldn't be measured and studied. Another reason proposed to support the idea that the mind couldn't be studied was the assertion that it is impossible for the mind to study itself.

Against this backdrop of skepticism regarding the possibility of studying the mind, Fechner, who had been thinking about this problem for many years, had an insight, the story goes, while lying in bed on the morning of October 22, 1850. His insight was that the mind and body should not be thought of as totally separate from one another but as two sides of a single reality (Wozniak, 1999). Most important, Fechner proposed that the mind could be studied by measuring the relationship between changes in physical stimulation (the body part of the relationship) and a person's experience (the mind part). This proposal was based on the observation that as physical stimulation is increased—for example, by increasing the *intensity* of a light—the person's perception of the *brightness* of the light also increases.

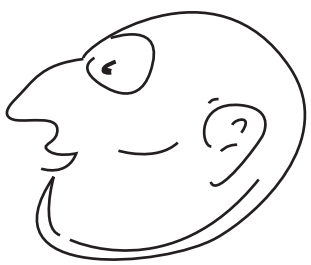

Figure 1.16 Man version of the rat–man stimulus. (Adapted from Bugelski & Alampay, 1961)

Ten years after having his insight about the mind, Fechner (1860/1966) published his masterpiece, *Elements of Psychophysics*, in which he proposed a number of methods for measuring stimulus–behavior relationships using psychophysics. One of the major contributions of *Elements of Psychophysics* was the proposal of three methods for measuring the threshold: the method of limits, the method of constant stimuli, and the method of adjustment. Taken together, these methods, which are called the **classical psychophysical methods**, opened the way for the founding of scientific psychology by providing methods to measure thresholds for perceiving sensory stimuli.

Every so often we will introduce a new method by describing it in a "Method" section. Students are sometimes tempted to skip these sections because they think the content is unimportant. However, you should resist this temptation because these methods are essential tools for the study of perception. These "Method" sections are often related to experiments described immediately afterward and also provide the background for understanding experiments that are described later in the book.

METHOD | Determining the Threshold

Fechner's classical psychophysical methods for determining the absolute threshold of a stimulus are the *method of limits*, *constant stimuli*, and *adjustment*. In the method of limits, the experimenter presents stimuli in either ascending order (intensity is increased) or descending order (intensity is decreased), as shown in **Figure 1.17**, which indicates the results of an experiment that measures a person's threshold for hearing a tone.

	1 ↓	2 ↑	3 ↓	4 ↑	5 ↓	6 ↑	7 ↓	8 ↑
Intensity								
103	Y		Y		Y		Y	
102	Y		Y		Y		Y	
101	Y		Y		Y		Y	Y
100	Y	Y	Y	Y	Y		Y	Y
99	Y	N	Y	N	Y	Y	Y	Y
98	N	N	Y	N	N	N	N	Y
97		N	N	N		N		N
96		N		N		N		N
95		N		N		N		N
Crossover values →	98.5	99.5	97.5	99.5	98.5	98.5	98.5	97.5

Threshold = Mean of crossovers = 98.5

Figure 1.17 The results of an experiment to determine the threshold using the method of limits. The dashed lines indicate the crossover point for each sequence of stimuli. The threshold—the average of the crossover values—is 98.5 in this experiment.

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On the first series of trials, the experimenter begins by presenting a tone with an intensity we will call 103, and the participant indicates by a "yes" response that he or she hears the tone. This response is indicated by a Y at an intensity of 103 in the far left column of the table. The experimenter then presents another tone, at a lower intensity, and the participant responds to this tone. This procedure continues, with the participant making a judgment at each intensity until the response is "no." This change from "yes" to "no," indicated by the dashed line, is the *crossover point*, and the threshold for this series is taken as the mean between 99 and 98, or 98.5. The next series of trials begins below the participant's threshold, so that the response is "no" on the first trial (intensity 95), and continues until "yes," when the intensity reaches 100. Notice that the crossover point when starting below the threshold is slightly different. Because the crossover points may vary slightly, this procedure is repeated a number of times, starting above the threshold half the time and starting below the threshold half the time. The threshold is then determined by calculating the average of all of the crossover points.

The method of constant stimuli is similar to the method of limits in that different stimulus intensities are presented one at a time, and the participant must respond whether they perceive it ("yes" or "no") on each trial. The difference is that in this method, the stimulus intensities are presented in random order, rather than in descending or ascending order. After presenting each intensity many times, the threshold is usually defined as the intensity that results in detection on 50 percent of trials.

The method of adjustment is slightly different in that the participant—rather than the experimenter—adjusts the stimulus intensity continuously until he or she can just barely detect the stimulus. For example, the participant might be asked to turn a knob to decrease the intensity of a sound until it can no longer be heard, and then to turn the knob back again so that the sound is just barely audible. This just barely audible intensity is taken as the threshold. The procedure is repeated numerous times, and the threshold is determined by taking the average setting.

The choice among these methods is usually determined by the degree of accuracy needed and the amount of time available. The method of constant stimuli is the most accurate method because it involves many observations and stimuli are presented in random order, which minimizes how presentation on one trial can affect the participant's judgment of the stimuli presented on the next trial. The disadvantage of this method is that it is time-consuming. The method of adjustment is faster because participants can determine their threshold in just a few trials by adjusting the stimulus intensity themselves.

While the method of limits, constant stimuli, and adjustment have a key role in history, it's important to note that they are still being used in perceptual research today to measure the absolute threshold of stimuli within the different senses under various conditions. Because of the impact of Fechner's contributions to our understanding of measuring thresholds, October 22, the date Fechner awoke with his insight that led to the founding of psychophysics, is known among psychophysical researchers as "Fechner Day." Add that date to your calendar if you're looking for another holiday to celebrate! (Another approach to measuring people's sensitivity, called "The Signal Detection Approach," is described in Appendix C, page 420.)

So far in this section, we have discussed how one might go about measuring the absolute threshold of a stimulus. But what if instead of measuring the detection threshold of just one stimulus ("Can you taste any salt in this stew?"), the researcher wants to measure the threshold *between* two stimuli? For instance, perhaps as you hone your cooking skills, you make a second batch of stew in which you start with the same amount of salt as the first batch. Now, you want to know how much more salt you need to add to the second batch to detect a difference in salt content between the two batches. In this case, you would be interested in the **difference threshold**—the smallest *difference* between two stimuli that enables us to tell the difference between them. In *Elements of Psychophysics*, Fechner not only proposed his psychophysical methods but also described the work of Ernst Weber (1795–1878), a physiologist who, a few years before the publication of Fechner's book, measured the difference threshold for different senses. See Appendix A (p. 417) for more details about difference thresholds.

Fechner's and Weber's methods not only made it possible to measure the ability to detect stimuli but also made it possible to determine *mechanisms* responsible for experiences. For example, consider what happens when you enter a dark place and then stay there for a while. At first you may not be able to see much (**Figure 1.18a**), but eventually your vision gets better and you are able to see light and objects that were invisible before (**Figure 1.18b**). This improved vision occurs because your threshold for seeing light is becoming smaller and smaller as you stay in the dark. By measuring how a person's threshold changes moment by moment, we can go beyond simply saying that "we see better when we spend time in the dark" to providing a quantitative description of what is happening as a person's ability to see improves. We will further discuss this particular aspect of vision (called the *dark adaptation curve*) in Chapter 3.

As significant as the methods for measuring thresholds are, we know that perception includes far more than just what happens at threshold. To understand the richness of perception, we need to be able to measure other aspects of sensory experience in addition to thresholds. In the next section, we describe techniques of measuring perception when a stimulus is above threshold.

Measuring Perception Above Threshold

In order to describe some of the ways perceptual researchers measure sensory experience above threshold, we will consider five questions about the perceptual world and the techniques used to answer these questions.

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(a)

(b)

Bruce Goldstein

Figure 1.18 (a) How a dark scene might be perceived when seen just after being in the light. (b) How the scene would be perceived after spending 10 to 15 minutes adapting to the dark. The improvement in perception after spending some time in the dark reflects a decrease in the threshold for seeing light.

Question 1: What Is the Perceptual Magnitude of a Stimulus? Technique: Magnitude Estimation

Things are big and small (an elephant; a bug), loud and soft (rock music; a whisper), intense and just perceptible (sunlight; a dim star), overpowering and faint (heavy pollution; a faint smell). Fechner was not only interested in measuring thresholds using the classical psychophysical methods; he was also interested in determining the relationship between physical stimuli (like rock music and a whisper) and the perception of their magnitude (like perceiving one to be *loud* and the other *soft*). Fechner created a mathematical formula relating physical stimuli and perception; modern psychologists have modified Fechner's equation based on a method not available in Fechner's time called **magnitude estimation** (Stevens, 1957, 1961).

METHOD | Magnitude Estimation

The procedure for a magnitude estimation experiment is relatively simple: The experimenter first presents a "standard" stimulus to the participant (let's say a sound of moderate intensity) and assigns it a value of, say, 10. The participant then hears sounds of different intensities, and is asked to assign a number to each of these sounds that is proportional to the loudness of the original sound. If the sound seems twice as loud as the standard, it gets a rating of 20; half as loud, a 5; and so on. Thus, the participant assigns a loudness value to each sound intensity. This number for "loudness" is the perceived magnitude of the stimulus.

The example of magnitude estimation used here is from the sense of hearing (judging the loudness of a sound), but as with other methods introduced in this chapter, the same technique can be applied to the other senses. As another example, the results of experiments using magnitude estimation to measure brightness (rather than loudness) are discussed in the "Something to Consider" section at the end of this chapter, and the mathematical formulas relating physical intensity and perceptual magnitude for brightness are discussed in Appendix B (p. 418).

Question 2: What Is the Identity of the Stimulus? Technique: Recognition Testing

When you name things, you are categorizing them (see page 9). The process of categorizing, which is called recognition, is measured in many different types of perceptual experiments. One application is testing the ability of people with brain damage. As we saw earlier in this chapter, Dr. P.'s brain damage led him to have trouble recognizing common objects, like a glove. The recognition ability of people with brain damage is tested by asking them to name objects or pictures of objects.

Recognition is also used to assess the perceptual abilities of people without brain damage. In Chapter 5 we will describe experiments that show that people can identify rapidly flashed pictures ("It's a docking area for boats lined with houses"), although seeing small details ("The second house has five rows of windows") requires more time (**Figure 1.19**).

Recognition is not only visual; it can also include hearing ("that's a car revving its engine"), touch ("that feels like an apple"), taste ("mmm, chocolate"), and smell ("that's a rose"). Because recognizing objects is so crucial for our survival, many perception researchers have shifted their emphasis from asking "What do you see?" (perception) to asking "What is that called?" (recognition).

Question 3: How Quickly Can I React to It? Technique: Reaction Time

The speed with which we react to something can be determined by measuring **reaction time**—the time between presentation of a stimulus and the

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Figure 1.19 A stimulus like those used in an experiment in which participants are asked to recognize a rapidly flashed scene. Participants can often recognize general properties of a rapidly flashed scene, such as "houses near water and a boat," but need more time to perceive the details.

person's reaction to it. An example of a reaction time experiment is to ask participants to keep their eyes fixed on the + in the display in **Figure 1.20a** and pay attention to location A on the left rectangle. Because the participant is *looking at* the + but *paying attention to* the top of the left rectangle, this task resembles what happens when you are looking in one direction but are paying attention to something off to the side.

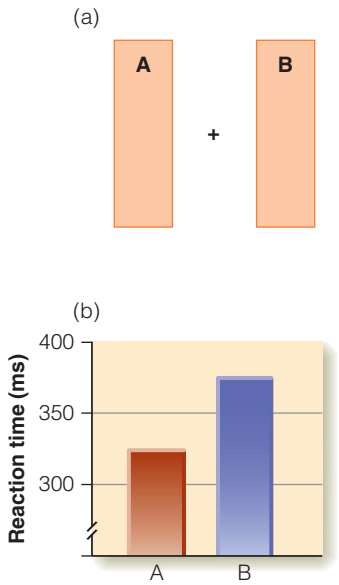

Figure 1.20 (a) A reaction time experiment in which the participant is told to look at the + sign, but pay attention to the location at A, and to push a button as quickly as possible when a dark target flashes anywhere on the display. (b) Reaction times in milliseconds, which indicates that reaction time was faster when the target was flashed at A, where the participant was attending, than when it was flashed at B, where the participant was not attending. (Data from Egly et al., 1994)

While directing attention to the top of the left rectangle, the participant's task was to push a button as quickly as possible when a dark target flashed anywhere on the display. The results, shown in **Figure 1.20b**, indicate that the participant responded more quickly when the target was flashed at A, where he or she was directing attention, compared to B, off to the side (Egly et al., 1994). These findings are relevant to a topic we will discuss in Chapter 7: How does talking on a cellphone while driving affect the ability to drive?

Question 4: How Can I Describe What Is Out There? Technique: Phenomenological Report

Look around. Describe what you see. You could name the objects you recognize, or you could describe the pattern of lights and darks and colors, or how things are arranged in space, or that two objects appear to be the same or different sizes or colors. Describing what is out there is called phenomenological report. For example, do you see a vase or two faces in **Figure 1.21**? We will see in Chapter 5 that displays like this are used to study how people perceive objects in front of backgrounds. Phenomenological reports are important because they define the perceptual phenomena we want to explain, and once a phenomenon is identified, we can then study it using other methods.

Question 5: How Can I Interact With It? Technique: Physical Tasks and Judgments

All of the other questions have focused on different ways of measuring what we perceive. This last question is concerned not with perception but with actions that follow perception (Step 7 of the perceptual process). Many perceptual researchers believe that one of the primary functions of perception is to enable us to take action within our environment. Look at it this way: Morg the caveman sees a dangerous tiger in the woods. He could stand there and marvel at the beauty of its fur, or the power of its legs, but if he doesn't take action by either hiding or getting away and the tiger sees him, his days of perceiving will be over. On a less dramatic level, we need to be able to see a saltshaker and then accurately reach across the table to pick it up, or navigate from one place on campus to another to get to class. Research on perception and action, which we will describe in Chapter 7, has participants carry out tasks that involve both perception and action, such as

Figure 1.21 Vase–face stimulus used to demonstrate how people perceive objects in front of a background.

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reaching for a target, navigating through a maze, or driving a car, under different conditions.

Physical tasks have also been studied by having people make judgments about tasks before they actually carry them out. For example, we will see in Chapter 7 that people with pain that makes walking difficult will estimate an object as being farther away than people who aren't in pain.

The examples above provide a hint as to the wide range of methods that are used in perception research. This book discusses research using the methods described above, plus others as well. Although we won't describe the details of the methods used in every experiment we consider, we will highlight the most important methods in "Method" sections like the ones on determining the threshold and on magnitude estimation in this chapter. Additionally, many physiological methods will be described in Methods sections in the chapters that follow. What will emerge as you read this book is a story in which important roles are played by both behavioral and physiological methods, which combine to create a more complete understanding of perception than is possible using either type of method alone.

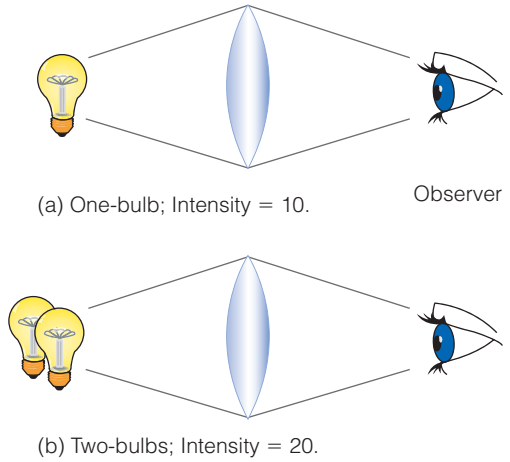

Figure 1.22 A participant (indicated by the eye) is viewing lights with different physical intensities. The two lights at (b) have twice the physical intensity as the single light at (a). However, when the participant is asked to judge brightness, which is a perceptual judgment, the light at (b) is judged to be only about 20 or 30 percent brighter than the light at (a).

SOMETHING TO CONSIDER:

Why Is the Difference Between Physical and Perceptual Important?

One of the most crucial distinctions in the study of perception is the distinction between *physical* and *perceptual*. To illustrate the difference, consider the two situations in **Figure 1.22**. In (a), the light from one light bulb with a physical intensity of 10 is focused into a person's eye. In (b), the light from two light bulbs, with a total intensity of 20, is focused into the person's eye. All of this so far has been *physical*. If we were to measure the intensities of the lights with a light meter, we would find that the person receives twice as much light in (b) as in (a).

But what does the person *perceive*? Perception of the light is measured not by determining the intensity but by determining *perceived brightness* using a method such as magnitude estimation (see page 16). What happens to brightness when we double the intensity from (a) to (b)? The answer is that (b) will appear brighter than (a), but not twice as bright. If the brightness is judged to be 10 for light (a), the brightness of light (b) will be judged to be about 12 or 13 (Stevens, 1962; also see Appendix B, page 418). Thus, there is not a one-to-one relationship between the physical intensity of the light and our perceptual response to the light.

As another example of the distinction between physical and perceptual, consider the **electromagnetic spectrum** in **Figure 1.23**. The electromagnetic spectrum is a band of energy ranging from gamma rays at the short-wave end of the spectrum

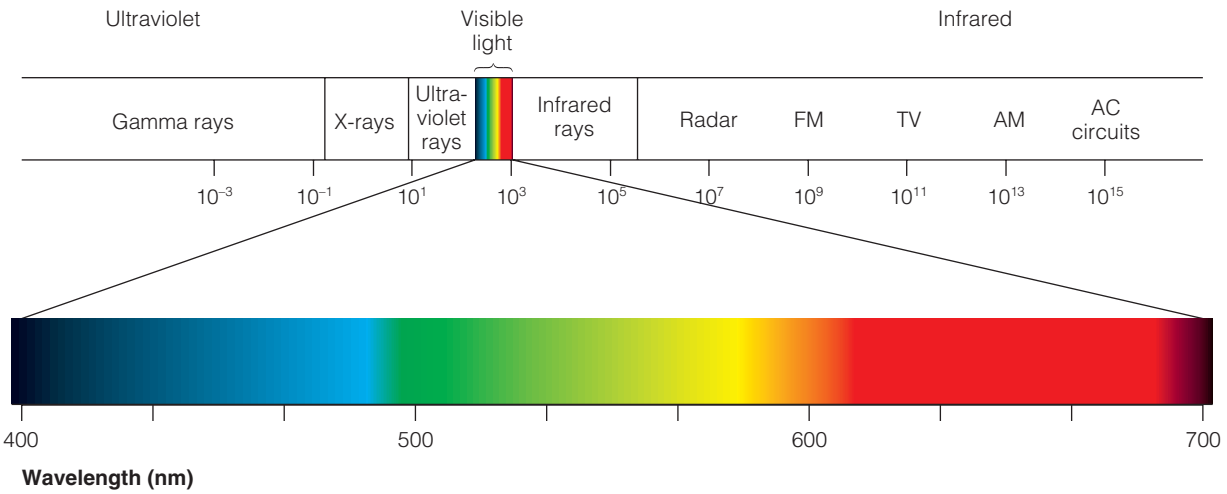

Figure 1.23 The electromagnetic spectrum, shown on top, stretches from gamma rays to AC circuits. The visible spectrum, shown exploded below, accounts for only a small part of the electromagnetic spectrum. We are blind to energy outside of the visible spectrum.

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to AM radio and AC circuits at the long-wave end. But we see just the small band of energy called visible light, sandwiched between the ultraviolet and infrared energy bands. We are blind to ultraviolet and shorter wavelengths (although hummingbirds can see ultraviolet wavelengths that are invisible to us). We also can't see at the high end of the spectrum, in the infrared and above, which is probably a good thing—imagine the visual clutter we would experience if we could see all of those cellphone conversations carrying their messages through the air!

What these examples illustrate is that what physical measuring instruments record and what we perceive are two different things. Ludy Benjamin, in his book *A History of Psychology* (1997), makes this point when he observes that "If changes in physical stimuli always resulted in similar changes in perception of those stimuli ... there would be no need for psychology; human perception could be wholly explained by the laws of the discipline of physics" (p. 120). But perception is psychology, not physics, and perceptual responses are not necessarily the same as the responses of physical measuring devices. We will, therefore, be careful, throughout this book, to distinguish between physical stimuli and the perceptual responses to these stimuli.

TEST YOURSELF 1.2

1. What was Fechner's contribution to psychology?
2. Describe the differences between the method of limits, the method of constant stimuli, and the method of adjustment.
3. Describe the five questions that can be asked about the world out there and the measurement techniques that are used to answer them.
4. Why is it important to distinguish between physical and perceptual?

THINK ABOUT IT

1. This chapter argues that although perception seems simple, it is actually extremely complex when we consider "behind the scenes" activities that are not obvious as a person is experiencing perception. Cite an example of a similar situation from your own experience, in which an "outcome" that might seem as though it was achieved easily actually involved a complicated process that most people are unaware of.
2. Describe a situation in which you initially thought you saw, heard, or felt something but then realized that your initial perception was in error. What was the role of bottom-up and top-down processing in this example of first having an incorrect perception and then realizing what was actually there?

KEY TERMS

Absolute threshold (p. 14)
Action (p. 9)
Bottom-up processing (data-based processing) (p. 10)
Categorize (p. 10)
Cerebral cortex (p. 8)
Classical psychophysical methods (p. 14)
Difference threshold (p. 15)
Distal stimulus (p. 7)
Electromagnetic spectrum (p. 18)
Frontal lobe (p. 9)
Grating acuity (p. 11)
Knowledge (p. 10)
Magnitude estimation (p. 16)
Method of adjustment (p. 15)
Method of constant stimuli (p. 15)
Method of limits (p. 14)
Neural processing (p. 8)
Oblique effect (p. 11)
Occipital lobe (p. 8)
Parietal lobe (p. 8)
Perceived magnitude (p. 16)
Perception (p. 4)
Perceptual process (p. 6)
Phenomenological report (p. 17)
Physiology–behavior relationship (p. 13)
Primary receiving area (p. 8)
Principle of representation (p. 7)
Principle of transformation (p. 7)
Proximal stimulus (p. 7)
Psychophysics (p. 11)
Rat–man demonstration (p. 10)
Reaction time (p. 16)
Recognition (p. 9)
Sensation (p. 5)
Sensory receptors (p. 7)
Stimulus–behavior relationship (p. 11)
Stimulus–physiology relationship (p. 11)
Temporal lobe (p. 8)
Thresholds (p. 14)
Top-down processing (knowledge-based processing) (p. 10)
Transduction (p. 8)
Visual form agnosia (p. 9)

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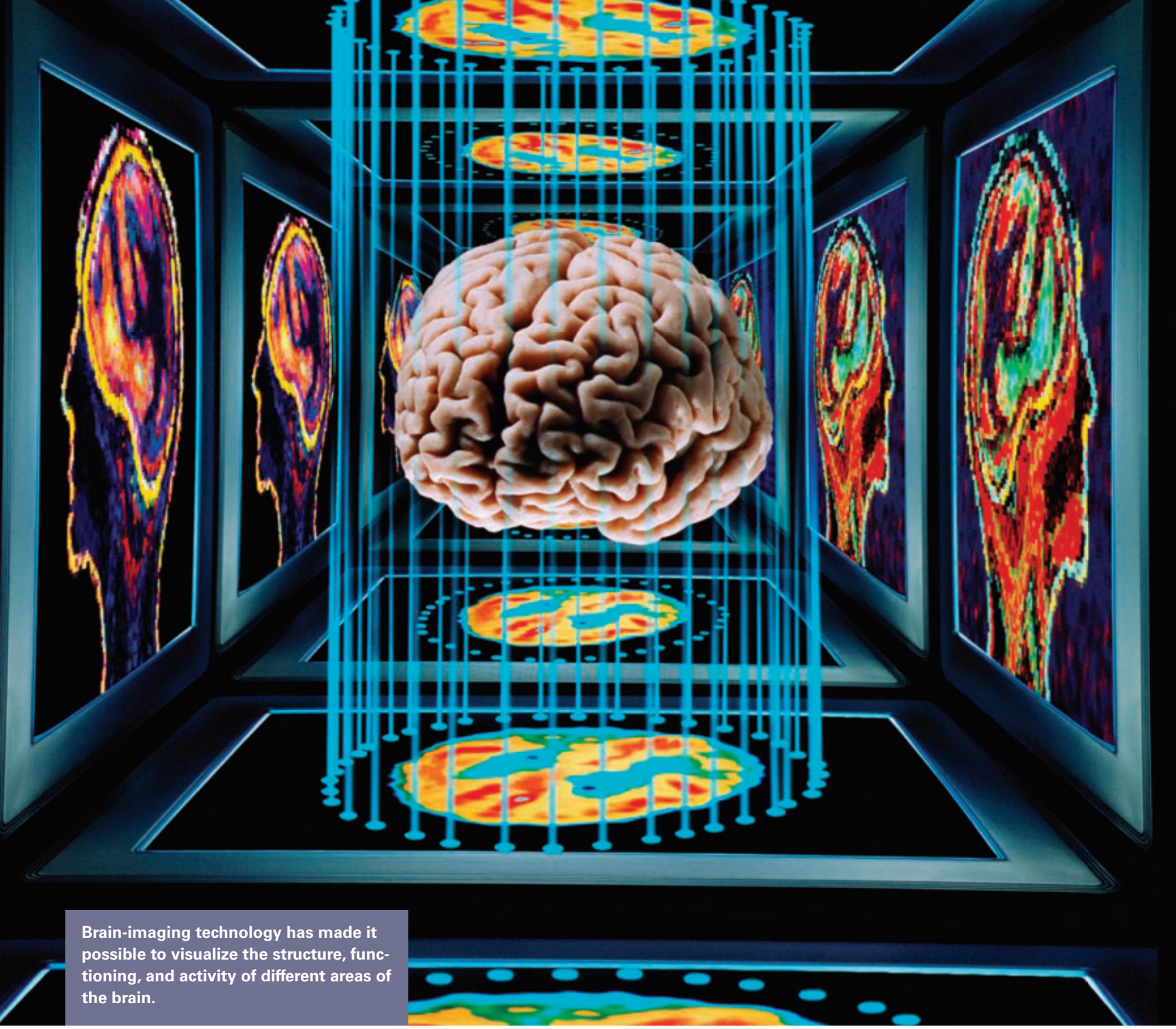

Brain-imaging technology has made it possible to visualize the structure, functioning, and activity of different areas of the brain.

Barry Blackman/Taxi/Getty Images

Learning Objectives

After studying this chapter, you will be able to ...

- Identify the key components of neurons and their respective functions.
- Explain how electrical signals are recorded from neurons and the basic properties of these signals.
- Describe the chemical basis of electrical signals in neurons.
- Describe how electrical signals are transmitted from one neuron to another.
- Understand the various ways that neurons can represent our sensory experiences.
- Explain how brain imaging can be used to create pictures of the locations of the brain's activity.
- Distinguish between structural and functional connectivity between brain areas and describe how functional connectivity is determined.
- Discuss the mind–body problem.

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CHAPTER 2

Basic Principles of Sensory Physiology

CHAPTER CONTENTS

2.1 Electrical Signals in Neurons
Recording Electrical Signals in Neurons
METHOD: The Setup for Recording From a Single Neuron
Basic Properties of Action Potentials
Chemical Basis of Action Potentials
Transmitting Information Across a Gap

2.2 Sensory Coding: How Neurons Represent Information
Specificity Coding
Sparse Coding
Population Coding
TEST YOURSELF 2.1

2.3 Zooming Out: Representation in the Brain
Mapping Function to Structure
METHOD: Brain Imaging
Distributed Representation
Connections Between Brain Areas
METHOD: The Resting State Method of Measuring Functional Connectivity
SOMETHING TO CONSIDER: The Mind–Body Problem
TEST YOURSELF 2.2
THINK ABOUT IT

Some Questions We Will Consider:

- How do neurons work, and how does neural firing underlie our perception? (p. 21)
- How do perceptual functions map onto the structure of the brain? (p. 30)
- How is brain activity measured both within a brain area and between different brain areas? (p. 31)

Two cars start at the same place and drive to the same destination. Car A takes an express highway, stopping only briefly for gas. Car B takes the "scenic" route—back roads that go through the countryside and small towns, stopping a number of times along the way to see some sights and meet some people. Each of Car B's stops can influence its route, depending on the information its driver receives. Stopping at a small-town general store, the driver of Car B hears about a detour up the road, so changes the route accordingly. Meanwhile, Car A is speeding directly to its destination.

The way electrical signals travel through the nervous system is more like Car B's journey. The pathway from receptors to brain is not a nonstop expressway. Every signal leaving a receptor travels through a complex network of interconnected signals, often meeting, and being affected by, other signals along the way.

What is gained by taking a complex, indirect route? If the goal were just to send a signal to the brain that a particular receptor had been stimulated, then the straight-through method would work. But the purpose of electrical signals in the nervous system goes beyond signaling that a receptor was stimulated. The information that reaches the brain and then continues its journey within the brain is much richer than this. As we will see in this and upcoming chapters, there are neurons in the brain that respond to certain stimuli like slanted lines, faces, movement across space in a specific direction, movement across the skin in a specific direction, or salty tastes. These neurons didn't achieve these properties by receiving signals through a straight-line transmission system from receptors to brain. They achieve these properties by *neural processing*—the interaction of the signals of many neurons (see page 8).

Because the activity of individual neurons and neural processing carried out by large numbers of neurons create our perceptual experiences, it is important to understand the basic mechanisms behind neural responding and neural processing. We begin by describing electrical signals in neurons.

2.1 Electrical Signals in Neurons

Electrical signals occur in structures called **neurons**, like the ones shown in **Figure 2.1**. The key components of neurons, shown in the neuron on the right in Figure 2.1, are the **cell body**, which

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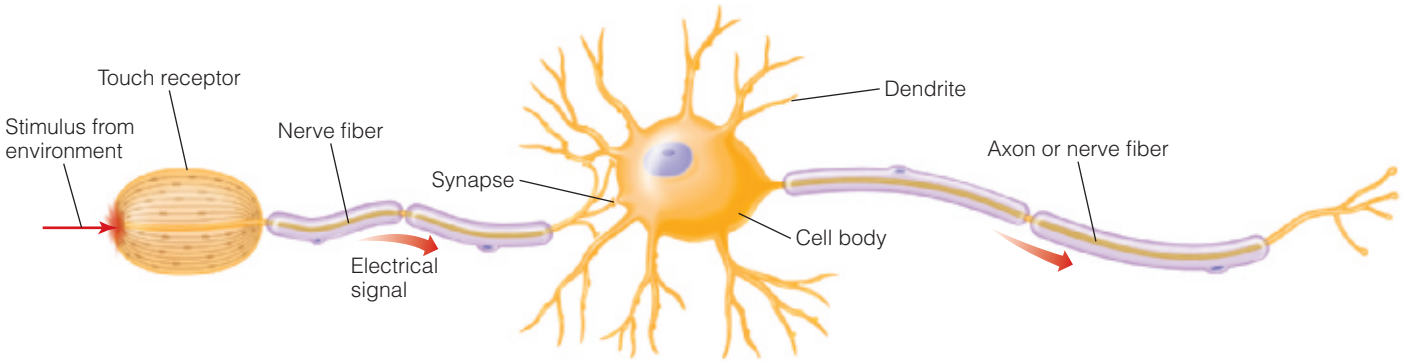

Figure 2.1 The neuron on the right consists of a cell body, dendrites, and an axon, or nerve fiber. The neuron on the left that receives stimuli from the environment has a receptor in place of the cell body.

contains mechanisms to keep the cell alive; dendrites, which branch out from the cell body to receive electrical signals from other neurons; and the axon, or nerve fiber, which is filled with fluid that conducts electrical signals. There are variations on this basic neuron structure: Some neurons have long axons; others have short axons or none at all. Especially important for perception are *sensory receptors* (see Figure 1.5), which are neurons specialized to respond to environmental stimuli. The receptor on the left in Figure 2.1 responds to touch stimuli.

Individual neurons do not, of course, exist in isolation. There are hundreds of millions of neurons in the nervous system, and each neuron is connected to many other neurons. As we will discuss later in this chapter, these connections are extremely important for perception. To begin our discussion of how neurons and their connections give rise to perception, we focus on individual neurons.

One of the most important ways of studying how electrical signals underlie perception is to record signals from single neurons. We can appreciate the importance of being able to record from single neurons by considering the following analogy: You walk into a large room in which hundreds of people are talking about a political speech they have just heard. There is a great deal of noise and commotion in the room as people react to the speech. Based on hearing this "crowd noise," all you can say about what is going on is that the speech seems to have generated a great deal of excitement. To get more specific information about the speech, you need to listen to what individual people are saying.

Just as listening to individual people provides valuable information about what is happening in a large crowd, recording from single neurons provides valuable information about what is happening in the nervous system. Recording from single neurons is like listening to individual voices. It is important to record from as many neurons as possible, of course, because just as individual people may have different opinions about the speech, different neurons may respond differently to a particular stimulus or situation.

The ability to record electrical signals from individual neurons ushered in the modern era of brain research, and in the 1950s and 1960s, development of sophisticated electronics and the availability of computers made possible more detailed analysis of how neurons function.

Recording Electrical Signals in Neurons

Electrical signals are recorded from the axons (or nerve fibers) of neurons using small electrodes to pick up the signals.

METHOD | The Setup for Recording From a Single Neuron

Figure 2.2a shows a typical setup used for recording from a single neuron. There are two electrodes: a *recording electrode,* shown with its recording tip inside the neuron,[1] and a *reference electrode,* located some distance away so it is not affected by the electrical signals. These two electrodes are connected to a meter that records the difference in charge between the tips of the two electrodes. This difference is displayed on a computer screen, like the one shown in **Figure 2.3**, which shows electrical signals being recorded from a neuron.

When the axon, or nerve fiber, is at rest, the difference in the electrical potential between the tips of the two electrodes is −70 millivolts (mV, where a millivolt is 1/1,000 of a volt), as shown on the right in Figure 2.2a. This means that the inside of the axon is 70 mV more negative than the outside. This value, which stays roughly the same as long as there are no signals in the neuron, is called the resting potential.

Figure 2.2b shows what happens when the neuron's receptor is stimulated so that a signal is transmitted down the axon. As the signal passes the recording electrode, the charge inside the axon rises to +40 mV compared to the outside. As the signal continues past the electrode, the charge inside the fiber reverses course and starts becoming negative again (**Figure 2.2c**), until it returns to the resting level (**Figure 2.2d**). This signal, identified by the predictable rise and fall of the charge inside the axon relative to the outside, is called the action potential, and lasts about 1 millisecond (ms, 1/1,000 second). When we refer to neurons as "firing," we are referring to the neuron having action potentials.

[1]In practice, most recordings are achieved with the tip of the electrode positioned just outside the neuron because it is technically difficult to insert electrodes into the neuron, especially if it is small. However, if the electrode tip is close enough to the neuron, the electrode can pick up the signals generated by the neuron.

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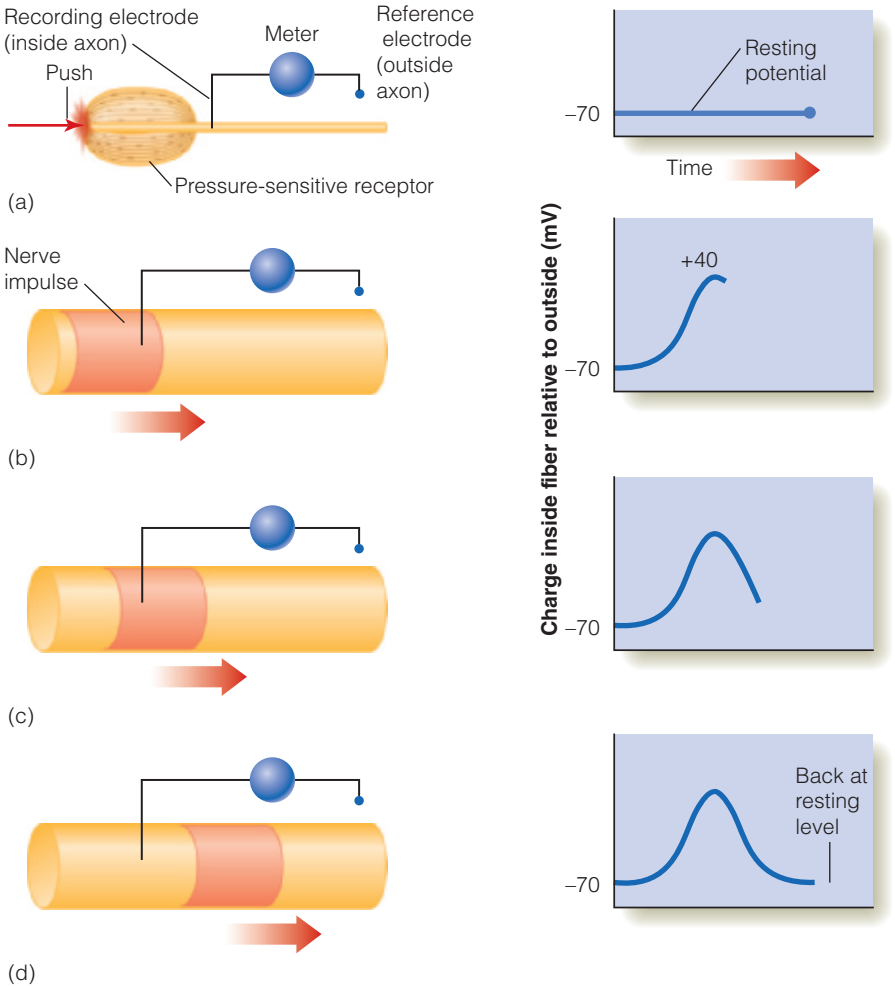

Figure 2.2 (a) When a nerve fiber is at rest, there is a difference in charge of −70 mV between the inside and the outside of the fiber. This difference, which is measured by the meter indicated by the blue circle, is displayed on the right. (b) As the nerve impulse, indicated by the red band, passes the electrode, the inside of the fiber near the electrode becomes more positive. This positivity is the rising phase of the action potential. (c) As the nerve impulse moves past the electrode, the charge inside the fiber becomes more negative. This is the falling phase of the action potential. (d) Eventually the neuron returns to its resting state.

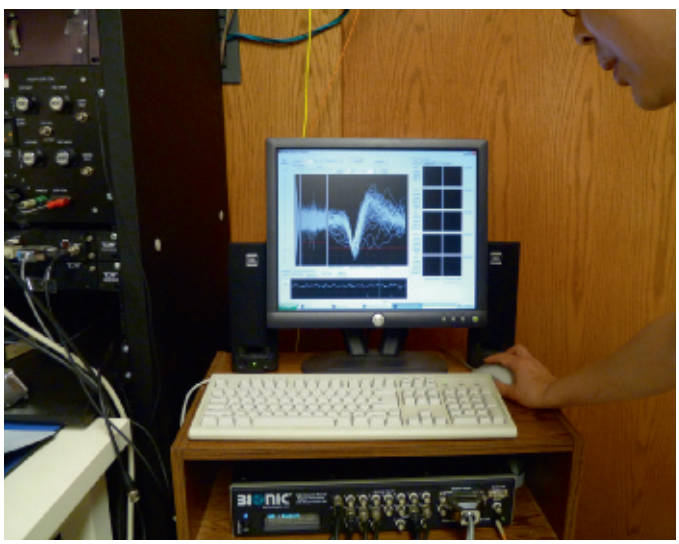

Figure 2.3 Electrical signals being displayed on a computer screen, in an experiment in which responses are being recorded from a single neuron. The signal on the screen shows the difference in voltage between two electrodes as a function of time. In this example, many signals are superimposed on one another, creating a thick white tracing. (Photographed in Tai Sing Lee's laboratory at Carnegie Mellon University)

Your experience of seeing the words on this page, hearing the sounds around you, and tasting your food all start with electrical signals in neurons. In this chapter we will first describe how individual neurons work, and will then consider how the activity of groups of neurons is related to perception. We begin by describing basic properties of the action potential and its chemical basis.

Basic Properties of Action Potentials

An important property of the action potential is that it is a propagated response—once the response is triggered, it travels all the way down the axon without decreasing in size. This means that if we were to move our recording electrode in Figure 2.2 to a position nearer the end of the axon, the electrical response would take longer to reach the electrode, but it would still be the same size (increasing from −70 to +40 mV) when it got there. This is an extremely important property of the action potential because it enables neurons to transmit signals over long distances.

Another property is that the action potential remains the same size no matter how intense the stimulus is. The three records in **Figure 2.4** represent the axon's response to three intensities of pushing on the skin. Each action potential appears as a sharp spike in these records because we have compressed the time scale

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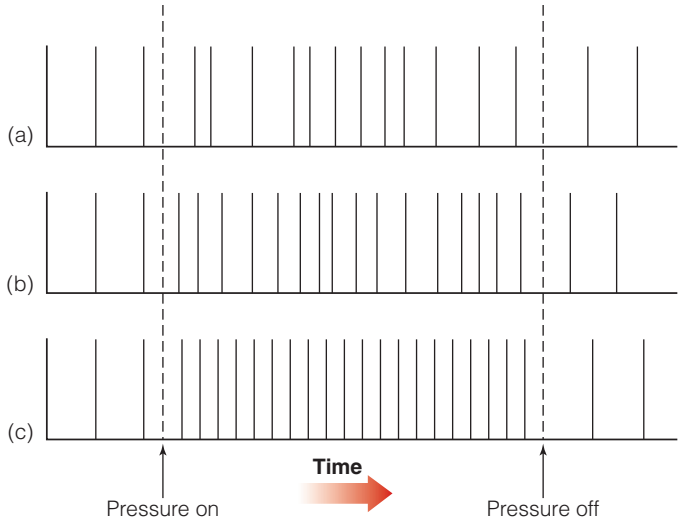

Figure 2.4 Response of a nerve fiber to (a) soft, (b) medium, and (c) strong stimulation. Increasing the stimulus strength increases both the *rate* and the *regularity* of nerve firing in this fiber, but has no effect on the *size* of the action potentials.

to display a number of action potentials. **Figure 2.4a** shows how the axon responds to gentle stimulation applied to the skin, and **Figures 2.4b** and **2.4c** show how the response changes as the pressure is increased. Comparing these three records leads to an important conclusion: Changing the stimulus intensity does not affect the *size* of the action potentials but does affect the *rate* of firing.

Although increasing the stimulus intensity can increase the rate of firing, there is an upper limit to the number of nerve impulses per second that can be conducted down an axon. This limit occurs because of another property of the axon called the refractory period—the interval between the time one nerve impulse occurs and the next one can be generated in the axon. Because the refractory period for most neurons is about 1 millisecond, the upper limit of a neuron's firing rate is about 500 to 800 impulses per second.

Another important property of action potentials is illustrated by the beginning of each of the records in Figure 2.4. Notice that a few action potentials are occurring even before the pressure stimulus is applied. Action potentials that occur in the absence of stimuli from the environment are called spontaneous activity. This spontaneous activity establishes a baseline level of firing for the neuron. The presence of stimulation usually causes an increase in activity above this spontaneous level, but under some conditions, which we will describe shortly, it can cause firing to decrease below the spontaneous level.

Chemical Basis of Action Potentials

What causes these rapid changes in charge that travel down the axon? Because this is a traveling electrical charge, we might be tempted to equate it to the electrical signals that are conducted along electrical power lines or the wires used for household appliances. But action potentials create electricity not in the dry environment of metal wires, but in the wet environment of the body.

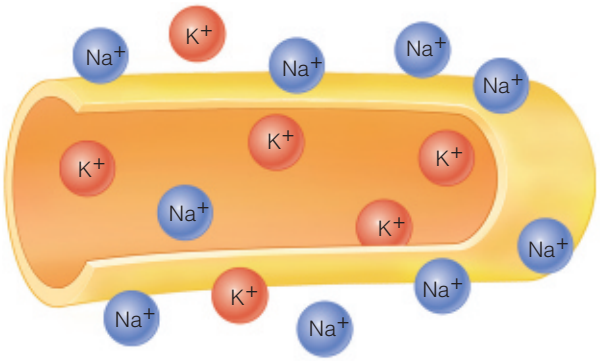

Figure 2.5 A nerve fiber showing the high concentration of sodium ions (Na^+) outside the fiber and potassium ions (K^+) inside the fiber. Other ions, such as negatively charged chlorine, are not shown.

The key to understanding the "wet" electrical signals transmitted by neurons is understanding the components of the neuron's liquid environment. Neurons are bathed in a liquid solution rich in ions, molecules that carry an electrical charge (**Figure 2.5**). Ions are created when molecules gain or lose electrons, as happens when compounds are dissolved in water. For example, adding table salt (sodium chloride, NaCl) to water creates positively charged sodium ions (Na^+) and negatively charged chlorine ions (Cl^-). The solution outside the axon of a neuron is rich in positively charged sodium (Na^+) ions, whereas the solution inside the axon is rich in positively charged potassium (K^+) ions. This distribution of ions across the neuron's membrane at rest is important to maintaining the −70 mV resting potential, as well as to the initiation of the action potential itself.

You can understand how these ions result in the action potential by imagining yourself just outside an axon next to a recording electrode (**Figure 2.6a**). (You will have to shrink yourself down to a very small size to do this!) Everything is quiet until incoming signals from other neurons trigger an action potential to begin traveling down the axon. As it approaches, you see positively charged sodium ions (Na^+) rushing into the axon (**Figure 2.6b**). This occurs because channels in the membrane that are selective to Na^+ have opened, which allow Na^+ to flow across the membrane and into the neuron. This opening of sodium channels represents an increase in the membrane's selective permeability to sodium, where permeability refers to the ease with which a molecule can pass through the membrane and selective means that the fiber is permeable to one specific type of molecule, Na^+ in this case, but not to others. The inflow of positively charged sodium causes an increase in the positive charge inside the axon from the resting potential of −70 mV until it reaches the peak of the action potential of +40 mV. An increase in positive charge inside the neuron is called depolarization. This quick and steep depolarization from −70 mV to +40 mV during an action potential is referred to as the rising phase of the action potential (Figure 2.6b).

Continuing your vigil, you notice that once the charge inside the neuron reaches +40 mV, the sodium channels close (the membrane becomes impermeable to sodium) and potassium channels open (the membrane becomes selectively permeable to potassium). Because there were more potassium ions (K^+) inside

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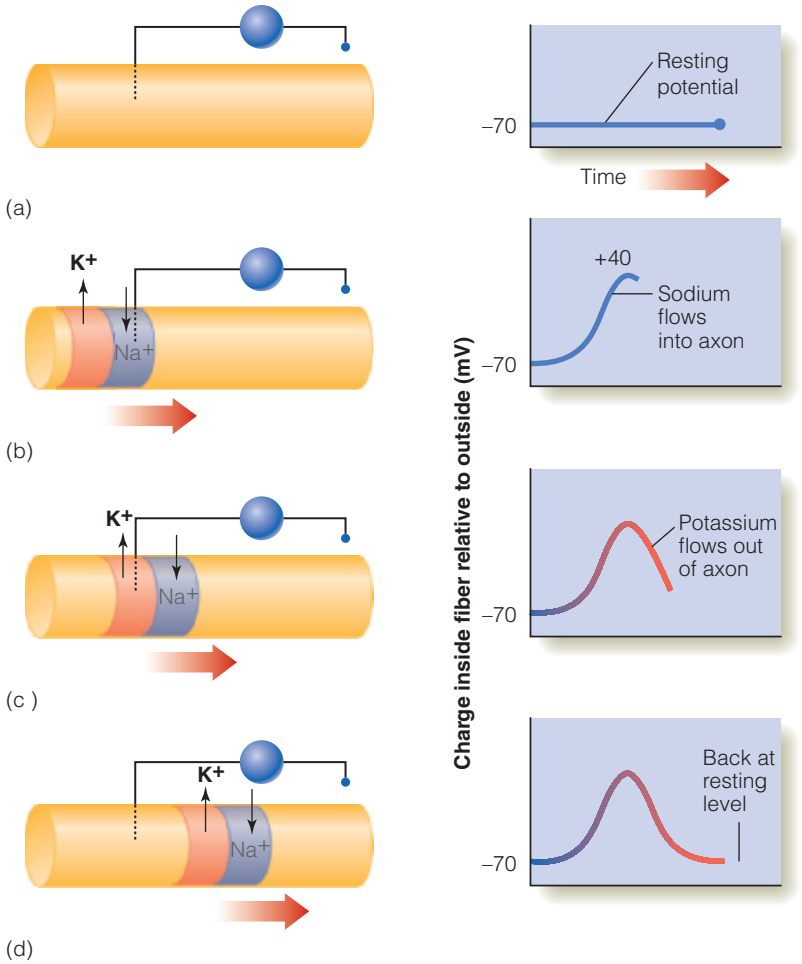

Figure 2.6 How the flow of sodium and potassium creates the action potential. (a) When the fiber is at rest, there is no flow of ions, and the record indicates the –70 mV resting potential. (b) Ion flow occurs when an action potential travels down the fiber. Initially, positively charged sodium (Na^+) flows into the axon, causing the inside of the neuron to become more positive (rising phase of the action potential). (c) Later, positively charged potassium (K^+) flows out of the axon, causing the inside of the axon to become more negative (falling phase of the action potential). (d) When the action potential has passed the electrode, the charge returns to the resting level.

than outside the neuron while at rest, positively charged potassium rushes out of the axon when the channels open, causing the charge inside the axon to become more negative. An increase in negative charge inside the neuron is called hyperpolarization. The hyperpolarization from +40 mV back to −70 mV is the falling phase of the action potential (**Figure 2.6c**). Once the potential has returned to the −70 mV resting level, the K^+ flow stops (**Figure 2.6d**), which means the action potential is over and the neuron is again at rest.

After reading this description of ion flow, students often ask why the sodium-in, potassium-out flow that occurs during the action potential doesn't cause sodium to build up inside the axon and potassium to build up outside. The answer is that a mechanism called the *sodium-potassium pump* keeps this buildup from happening by continuously pumping sodium out and potassium into the fiber.

Transmitting Information Across a Gap

We have seen that action potentials caused by sodium and potassium flow travel down the axon without decreasing in size. But what happens when the action potential reaches the end of the axon? How is the action potential's message transmitted to other neurons? The problem is that there is a very small space between neurons, known as a synapse (**Figure 2.7**). The discovery of the synapse raised the question of how the electrical

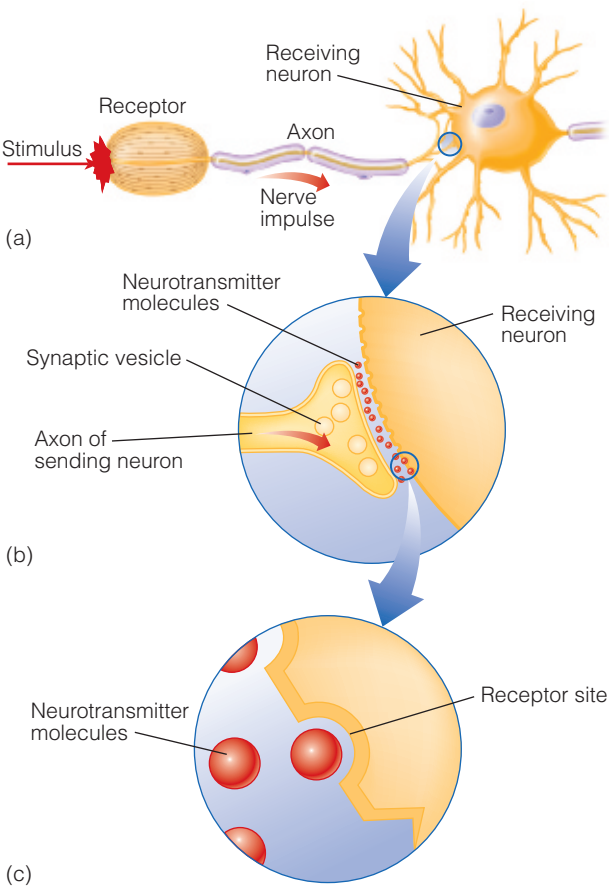

Figure 2.7 Synaptic transmission from one neuron to another. (a) A signal traveling down the axon of a neuron reaches the synapse at the end of the axon. (b) The nerve impulse causes the release of neurotransmitter molecules (red) from the synaptic vesicles of the sending neuron. (c) The neurotransmitters fit into receptor sites that are shaped like the transmitter and cause a voltage change in the receiving neuron.

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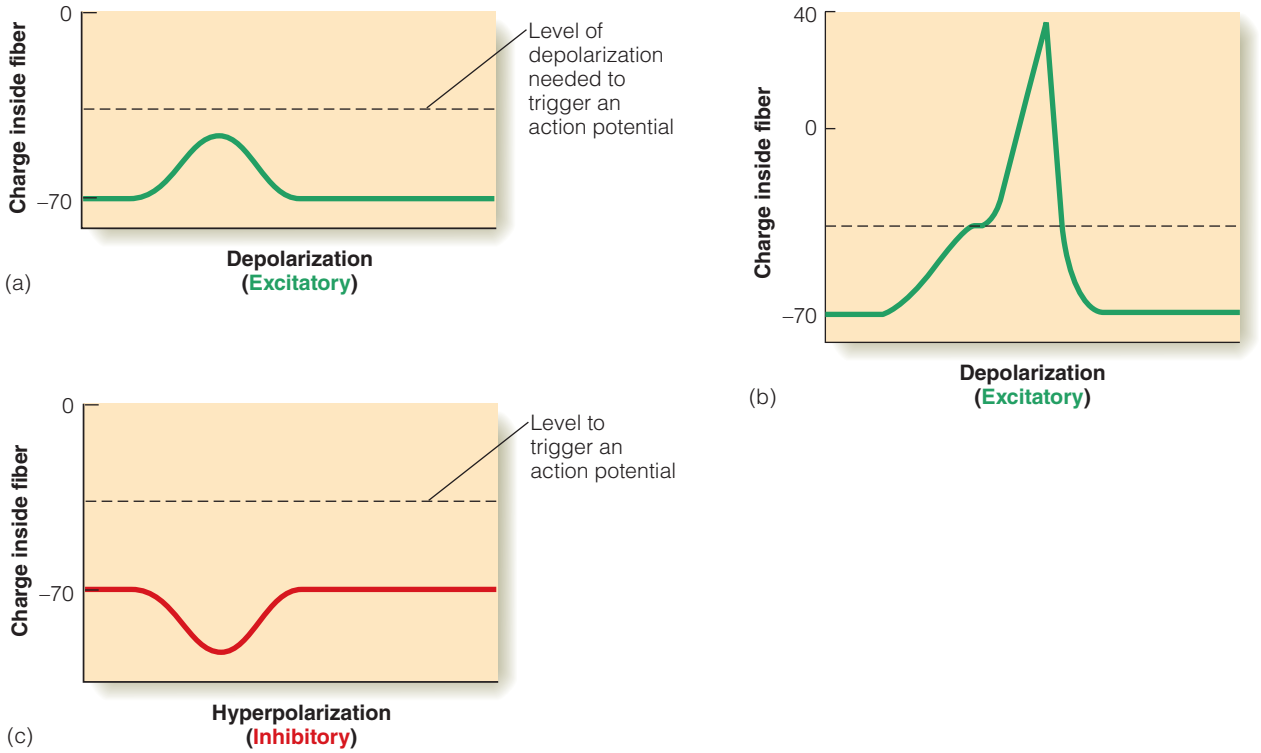

Figure 2.8 (a) Excitatory transmitters cause depolarization, an increased positive charge inside the neuron. (b) When the level of depolarization reaches threshold, indicated by the dashed line, an action potential is triggered. (c) Inhibitory transmitters cause hyperpolarization, an increased negative charge inside the axon.

signals generated by one neuron are transmitted across the space separating the neurons. As we will see, the answer lies in a remarkable chemical process that involves molecules called *neurotransmitters*.

Early in the 1900s, it was discovered that when action potentials reach the end of a neuron, they trigger the release of chemicals called **neurotransmitters** that are stored in structures called *synaptic vesicles* at the end of the sending neuron (**Figure 2.7b**). The neurotransmitter molecules flow into the synapse to small areas on the receiving neuron called **receptor sites** that are sensitive to specific neurotransmitters (**Figure 2.7c**). These receptor sites exist in a variety of shapes that match the shapes of particular neurotransmitter molecules. When a neurotransmitter makes contact with a receptor site matching its shape, it activates the receptor site and triggers a voltage change in the receiving neuron. A neurotransmitter is like a key that fits a specific lock. It has an effect on the receiving neuron only when its shape matches that of the receptor site.

Thus, when an electrical signal reaches the synapse, it triggers a chemical process that causes a new electrical signal in the receiving neuron. The nature of this signal depends on both the type of transmitter that is released and the nature of the receptor sites in the receiving neuron. Two types of responses can occur at these receptor sites, *excitatory* and *inhibitory*. An **excitatory response** occurs when the neuron becomes depolarized, and thus the inside of the neuron becomes more positive. **Figure 2.8a** shows this effect. Notice, however, that this response is much smaller than the depolarization that happens during an action potential. To generate an action potential, enough excitation must occur to increase depolarization to the level indicated by the dashed line.

How does the receiving neuron get enough excitation to reach this level? The answer is that it might take more than one excitatory response, such as what occurs when multiple neurotransmitters from a number of incoming neurons all reach the receptor sites of the receiving neuron at once. If the resulting depolarization is large enough, an action potential is triggered (**Figure 2.8b**). Depolarization is an excitatory response because it causes the charge to change in the direction that triggers an action potential.

An **inhibitory response** occurs when the inside of the neuron becomes more negative, or hyperpolarized. **Figure 2.8c** shows this effect. Hyperpolarization is an inhibitory response because it causes the charge inside the axon to move away from the level of depolarization, indicated by the dashed line, needed to generate an action potential.

We can summarize this description of the effects of excitation and inhibition as follows: Excitation increases the chances that a neuron will generate action potentials and is associated with increasing rates of nerve firing. Inhibition decreases the chances that a neuron will generate action potentials and is associated with lowering rates of nerve firing. Since a typical neuron receives both excitation and inhibition,

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the response of the neuron is determined by the interplay of excitation and inhibition, as illustrated in **Figure 2.9**. In **Figure 2.9a**, excitation (E) is much stronger than inhibition (I), so the neuron's firing rate is high. However, as inhibition becomes stronger and excitation becomes weaker, the neuron's firing decreases, until in **Figure 2.9e**, inhibition has eliminated the neuron's spontaneous activity and has decreased firing to zero.

Why does inhibition exist? If one of the functions of a neuron is to transmit its information to other neurons, what would be the point of decreasing or eliminating firing in the next neuron? The answer is that the function of neurons is not only to transmit information but also to *process* it, and, as we will see in Chapter 3, both excitation and inhibition are involved in this processing.

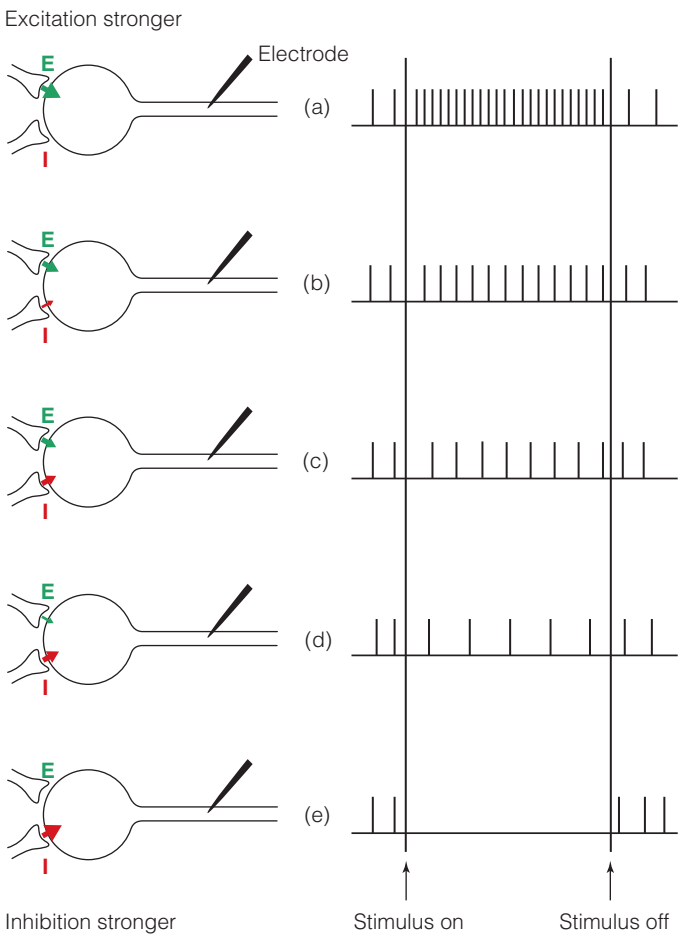

Figure 2.9 Effect of excitatory (E) and inhibitory (I) input on the firing rate of a neuron. The amount of excitatory and inhibitory input to the neuron is indicated by the size of the arrows at the synapse. The responses recorded by the electrode are indicated by the records on the right. The firing that occurs before the stimulus is presented is spontaneous activity. In (a), the neuron receives only excitatory transmitter, which causes the neuron to fire. In (b) to (e), the amount of excitatory transmitter decreases while the amount of inhibitory transmitter increases. As inhibition becomes stronger relative to excitation, firing rate decreases, until eventually the firing rate becomes zero.

2.2 Sensory Coding: How Neurons Represent Information

Now that we have an understanding of the basics of neural functioning, we can go one step further and think about how these neural processes underlie perception. How is it that a neuron "represents" information, like the taste of the salt in your stew? Is there a "salty" neuron in your brain that only fires in response to salt, and so causes you to perceive "saltiness"? Or does the pattern of firing of a group of neurons in one brain area, or perhaps many brain areas, result in our perception of saltiness? The problem of neural representation for the senses has been called the problem of **sensory coding**, where the sensory code refers to how neurons represent various characteristics of the environment.

Specificity Coding

One way in which neurons can represent sensory information is demonstrated in the "salty neuron" example above—the idea that one neuron can represent one perceptual experience, like the taste of salt. This notion of a specialized neuron that responds only to one concept or stimulus is called **specificity coding**. An example of specificity coding from the sense of vision is illustrated in **Figure 2.10**, which shows how a number of neurons respond to three different faces (the actual firing rates don't matter; they're made up for the sake of this example). Only neuron #4 responds to Bill's face, only #9 responds to Mary's face, and only #6 responds to Raphael's face. Also note that the neuron specialized to respond only to Bill, which we can call a "Bill neuron," does not respond to Mary or Raphael. In addition, other faces or types of objects would not affect this neuron. It fires only in response to Bill's face.

This idea that one neuron can represent one stimulus or concept, such as a face, dates back to the 1960s (Konorski, 1967; see also Barlow, 1972; Gross, 2002). At that time, Jerome Lettvin proposed the somewhat tongue-in-cheek idea that neurons could be so specific that there could be one neuron in your brain that fires only in response to, say, your grandmother. This highly specific type of neuron, dubbed by Lettvin as a **grandmother cell**, would respond to your grandmother "... whether animate or stuffed, seen from before or behind, upside down or on a diagonal or offered by caricature, photograph or abstraction" (Lettvin, as quoted in Gross, 2002).

According to Lettvin, even just thinking about the *idea* of your grandmother, not just the visual input, could make your grandmother cell fire. Along this reasoning, you would also have a "grandmother cell" for every face, stimulus, and concept that you've ever encountered—a specific neuron to represent your professor, one for your best friend, one for your dog, and so on. Perhaps you even have grandmother cells that respond

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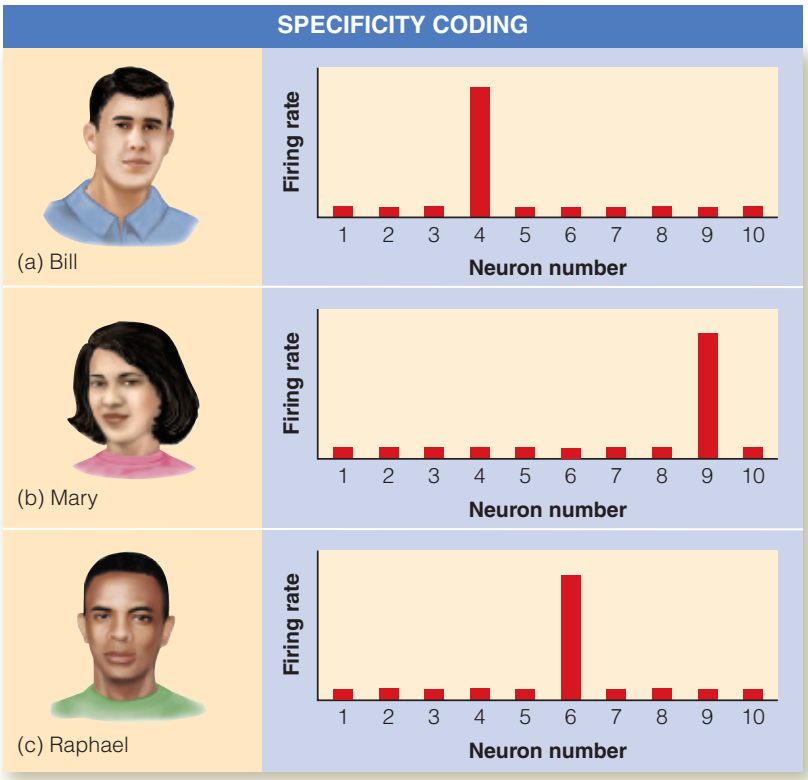

Figure 2.10 Specificity coding, in which each face causes a different neuron to fire. Firing of neuron 4 signals "Bill"; neuron 9 signals "Mary"; neuron 6 signals "Raphael."

to specific information in other senses as well, like one neuron per song that you know or food that you've eaten. Could it be that we have such specific representations of stimuli and concepts that we've encountered?

Evidence that provided some insight into this question came from R. Quian Quiroga and colleagues (2005; 2008) who recorded from the temporal lobe of patients undergoing brain surgery for epilepsy. (Stimulating and recording from neurons is a common procedure before and during brain surgery, because it makes it possible to determine the exact layout of a particular person's brain.) These patients were presented with pictures of famous people from different viewpoints, as well as other things such as other faces, buildings, and animals, in order to see how the neurons responded. Not surprisingly, a number of neurons responded to some of these stimuli. What was surprising, however, was that some neurons responded to a number of different views of just one person or building, or to a number of ways of representing that person or building.

For example, **Figure 2.11** shows a particular neuron that responded to pictures of the actor Steve Carell and not to other people's faces (Quiroga et al., 2008). Neurons were also found that responded to just the actress Halle Berry, including pictures of her from different films, a sketch drawing of her, and even just the words "Halle Berry" (Quiroga et al., 2005). Thus, these neurons were not just responding to the visual input of the famous person's face, but also to the *concept* of that particular person. Likewise, other neurons were found that responded just to certain buildings, like the Sydney Opera House, and not any other buildings or objects, indicating that these specific cells can be found not just for people but for other objects as well.

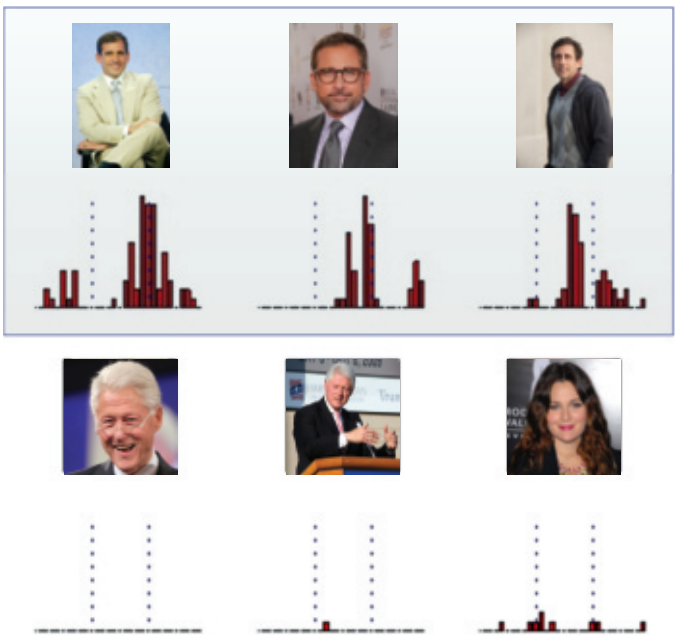

Figure 2.11 Records from a neuron in the temporal lobe that responded to different pictures of Steve Carell similar to the ones shown here (top records) but which did not respond to pictures of other well-known people (bottom records). (From Quiroga et al., 2008)

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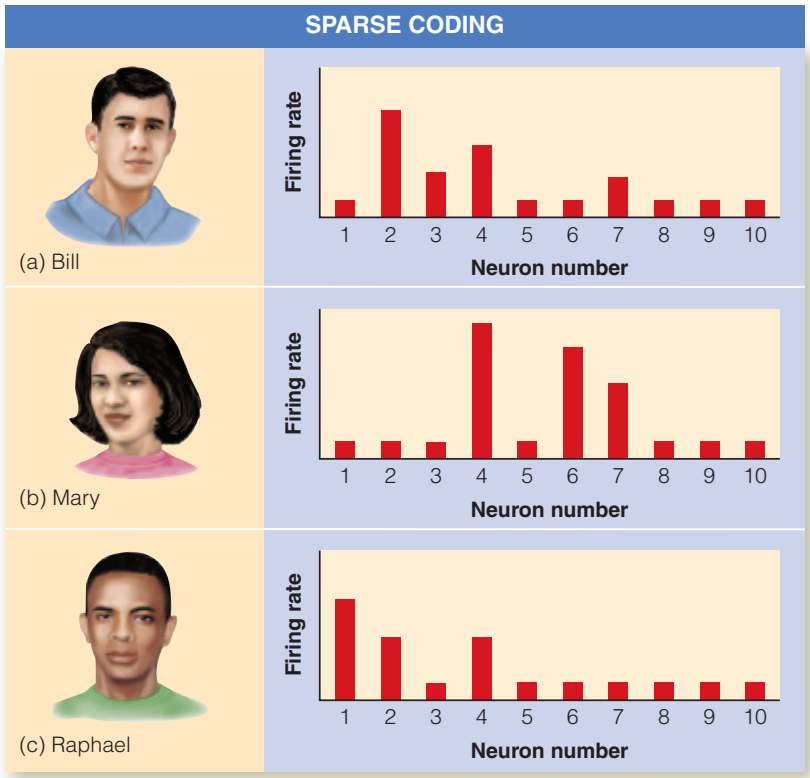

Figure 2.12 Sparse coding, in which each face's identity is indicated by the pattern of firing of a small number of neurons. Thus, the pattern created by neurons 2, 3, 4, and 7 signals "Bill"; the pattern created by 4, 6, and 7 signals "Mary"; the pattern created by 1, 2, and 4 signals "Raphael."

At this point, you might be thinking that Quiroga and coworkers' study provides evidence for grandmother cells. After all, these neurons were responding to highly specific stimuli! While this finding does seem *consistent* with the idea of grandmother cells, it does not *prove* that they exist. The researchers themselves even say that their study doesn't necessarily support the notion of grandmother cells. In fact, Quiroga and colleagues point out that they had only 30 minutes to record from these neurons, and that if more time were available, it is likely that they would have found other faces, places, or objects that would have caused these neurons to fire. In other words, the "Steve Carell neuron" might actually have been responsive to other faces or objects as well, had more options been tested.

In fact, the idea of grandmother cells is not typically accepted by neuroscientists today, given the lack of confirmatory evidence and its biological implausibility. Do we really have one neuron to represent every single concept we've encountered? It's unlikely, given how many neurons would be required. An alternative to the idea of specificity coding is that a number of neurons—rather than just one—are involved in representing a perceptual experience.

Sparse Coding

In their 2008 article, Quiroga and coworkers proposed that *sparse coding*, rather than specificity coding, was more likely to underlie their results. Sparse coding occurs when a particular stimulus is represented by a pattern of firing of only a small group of neurons, with the majority of neurons remaining silent. Going back to our example of using faces as stimuli, as shown in **Figure 2.12a**, sparse coding would represent Bill's face by the pattern of firing of a few neurons (neurons 2, 3, 4, and 7). Mary's face would be signaled by the pattern of firing of a few different neurons (neurons 4, 6, and 7; **Figure 2.12b**), but possibly with some overlap with the neurons representing Bill, and Raphael's face would have yet another pattern (neurons 1, 2, and 4; **Figure 2.12c**). Notice that a particular neuron can respond to more than one stimulus. For example, neuron #4 responds to all three faces, although most strongly to Mary's.

There is evidence that the code for representing objects in the visual system, tones in the auditory system, and odors in the olfactory system may involve a pattern of activity across a relatively small number of neurons, as sparse coding suggests (Olshausen & Field, 2004).

Population Coding

While sparse coding proposes that the pattern of firing across a *small* number of neurons underlies neural representation, population coding proposes that our experiences are represented by the pattern of firing across a *large* number of neurons. According to this idea, Bill's face might be represented by the pattern of firing shown in **Figure 2.13a**, Mary's face by a different pattern (**Figure 2.13b**), and Raphael's face by another pattern (**Figure 2.13c**). An advantage of population coding is that a large number of stimuli can be represented, because large groups of neurons can create a huge number of different patterns. As we will see in upcoming chapters, there

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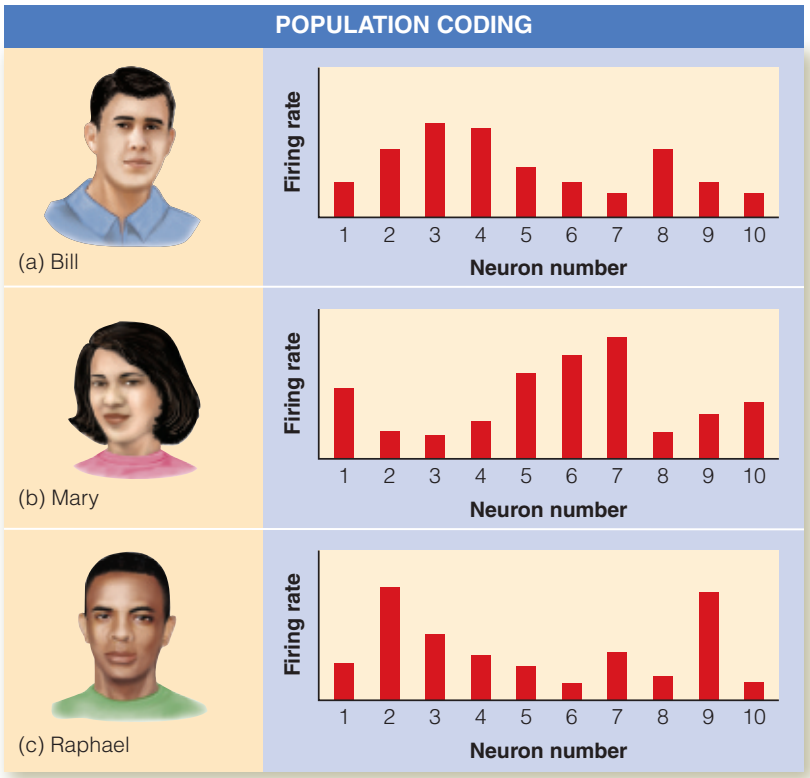

Figure 2.13 Population coding, in which the face's identity is indicated by the pattern of firing of a large number of neurons.

is good evidence for population coding in each of the senses, and for other cognitive functions as well.

Returning to the question about how neural firing can represent perception, we can state that part of the answer is that perceptual experiences—such as the experience of the aroma of cooking or the appearance of the objects on the table in front of you—are represented by the pattern of firing of groups of neurons. Sometimes the groups are small (sparse coding), sometimes large (population coding).

TEST YOURSELF 2.1

1. Describe the basic structure of a neuron.
2. Describe how to record electrical signals from a neuron.
3. What are some of the basic properties of action potentials?
4. Describe what happens when an action potential travels along an axon. In your description, indicate how the charge inside the fiber changes, and how that is related to the flow of chemicals across the cell membrane.
5. How are electrical signals transmitted from one neuron to another? Be sure you understand the difference between excitatory and inhibitory responses.
6. What is a grandmother cell? Describe Quiroga and colleagues' experiments on recordings from neurons in patients undergoing surgery for epilepsy.
7. What is the sensory code? Describe specificity, sparse, and population coding. Which types of coding are most likely to operate in sensory systems?

2.3 Zooming Out: Representation in the Brain

So far in this chapter, we've been focusing mainly on how neural firing "represents" information that's out there in the world, such as a face. But as we'll see throughout this book as we explore each of the senses, perception goes beyond individual neurons or even groups of neurons. To get a more complete picture of the physiology of perception, we must zoom out from neurons and consider representation in the brain more broadly, including different brain areas and the connections between those areas.

Mapping Function to Structure

How do perceptual functions, like perceiving faces, map onto the structure of the brain? The general question of how different functions map onto different brain areas can be dated all the way back to the 18th century with German physiologist Franz Joseph Gall and his colleague Johann Spurzheim. Using prison inmates and mental hospital patients as his participants, Gall claimed to observe a correlation between the shape of a person's skull and their abilities and traits, which he called "mental faculties." Based on his observations, Gall concluded that there were about 35 different mental faculties that could be mapped onto different brain areas based on the bumps and contours on the person's skull, as in **Figure 2.14**—an approach that Spurzheim called phrenology. For instance,

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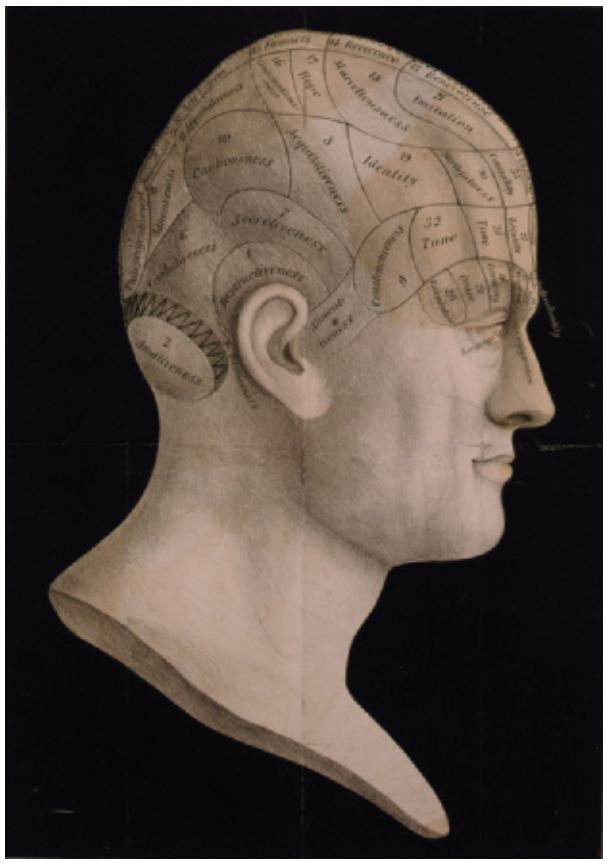

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Figure 2.14 How different functions map onto the structure of the head, according to phrenology.

a ridge on the back of your head might mean that you're a loving person, while a bump on the side means that you're good at musical perception.

Although phrenology has now been debunked as a method, it was the first proposal that different functions map onto different areas of the brain—a concept that is still discussed today. The idea that specific brain areas are specialized to respond to specific types of stimuli or functions is called **modularity**, with each specific area called a **module**.

Early evidence supporting modularity of function came from case studies of humans with brain damage. One such historical case study was conducted by French physician Pierre Paul Broca (1824–1890), who saw a patient with a very specific behavioral deficit: the patient could only speak the word "tan," although his speech comprehension and other cognitive abilities appeared to be intact. Examination of Tan's brain after his death showed that he had a lesion to his left frontal lobe (**Figure 2.15**). Soon thereafter, Broca saw other patients with similar defects in speech production who had damage to that same area of the brain. Broca therefore concluded that this area was the speech production area, and it came to be known as **Broca's area**. Another early researcher, Carl Wernicke (1848–1905) identified an area in the temporal lobe which was involved in understanding speech, and which came to be known as **Wernicke's area** (Figure 2.15).

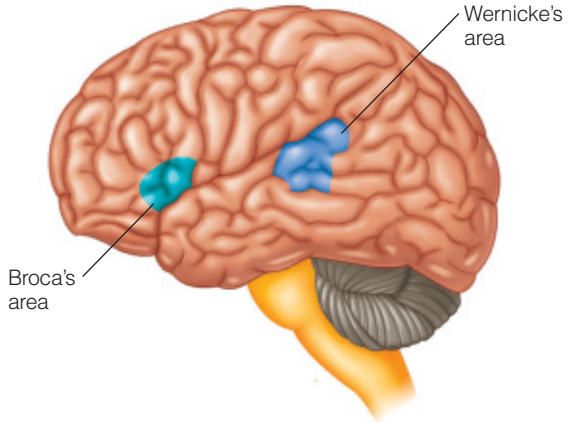

Figure 2.15 Broca's and Wernicke's areas. Broca's area is in the frontal lobe, and Wernicke's area is in the temporal lobe.

Broca's and Wernicke's areas provided early evidence for modularity, and since Broca's and Wernicke's pioneering research, there have been many other studies relating the location of brain damage to specific effects on behavior—a field now known as **neuropsychology**. We will describe more examples of neuropsychological case studies throughout this book, including more on Broca and Wernicke in Chapter 14.

While neuropsychology has provided evidence for modularity, studying patients with brain damage is difficult for numerous reasons, including the fact that the extent of each patient's damage can differ greatly. A more controlled way that modularity has been studied is by recording brain responses in neurologically normal humans using **brain imaging**, which makes it possible to create pictures of the location of the brain's activity.

METHOD | **Brain Imaging**

In the 1980s, a technique called magnetic resonance imaging (MRI) made it possible to create images of structures within the brain. Since then, MRI has become a standard technique for detecting tumors and other brain abnormalities. While this technique is excellent for revealing brain structures, it doesn't indicate neural activity. Another technique, functional magnetic resonance imaging (fMRI), has enabled researchers to determine how various types of cognitions, or *functions* (hence the "functional" part of functional MRI), activate different areas of the brain.

Functional magnetic resonance imaging takes advantage of the fact that blood flow increases in areas of the brain that are activated. The measurement of blood flow is based on the fact that hemoglobin, which carries oxygen in the blood, contains a ferrous (iron) molecule and therefore has magnetic properties. If a magnetic field is presented to the brain, the hemoglobin molecules line up, like tiny magnets. Areas of the brain that are more active consume more oxygen, so the hemoglobin molecules lose some

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of the oxygen they are transporting, which makes them more magnetic and increases their response to the magnetic field. The fMRI apparatus, also known as the "scanner," determines the relative activity of various areas of the brain by detecting changes in the magnetic response of the hemoglobin.

The setup for an fMRI experiment is shown in **Figure 2.16a**, with the person laying down such that their head is in the scanner. As a person engages in a task, such as listening to certain sounds, the activity of the brain is recorded. Importantly, fMRI is limited in that it can't record activity from individual neurons. Instead, what's being recorded is activity in subdivisions of the brain called *voxels*, which are small cube-shaped areas of the brain about 2 or 3 mm on a side. Due to their size, each voxel contains many neurons. Voxels are not brain structures but are simply small units of analysis created by the fMRI scanner. One way to think about voxels is that they are like the small square pixels that make up the image on your computer screen, but because the brain is three-dimensional, voxels are small cubes rather than small squares.

Figure 2.16b shows the results of an fMRI scan. Increases or decreases in brain activity associated with cognitive activity are indicated by colors, with specific colors indicating the amount of activation; usually "hotter" colors like red indicate higher activation, while "cooler" colors like blue indicate lower activation. Note how the brain appears pixelated in Figure 2.16b; each of those small units is a voxel!

It is important to realize that these colored areas do not appear as the brain is being scanned. They are determined by a calculation in which brain activity that occurred during the cognitive task is compared to baseline activity (like while the participant is at rest) or a different task. The results of this calculation, which indicate increases or decreases in activity in specific areas of the brain, are then converted into colored displays like the one in Figure 2.16b.

Many researchers have used brain imaging techniques like fMRI in an attempt to map a certain function onto a specific area of the brain. One example of this from speech perception (continuing from our discussion of Broca) is a study by Belin and coworkers (2000) which asked whether there is a brain area that responds specifically when you hear a voice, compared to when you hear other sounds. The participants reclined in the fMRI scanner and passively listened to vocal sounds on some trials and non-vocal sounds, like environmental sounds, on other trials. The results of the study revealed an area in the temporal lobe—the superior temporal sulcus (STS), (**Figure 2.17**)—that was activated significantly more in response to vocal sounds than non-vocal sounds. This area was therefore dubbed the "voice area" of the brain, given its highly specialized response.

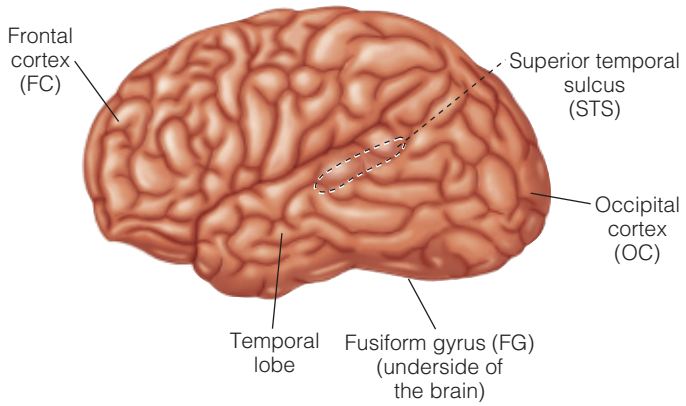
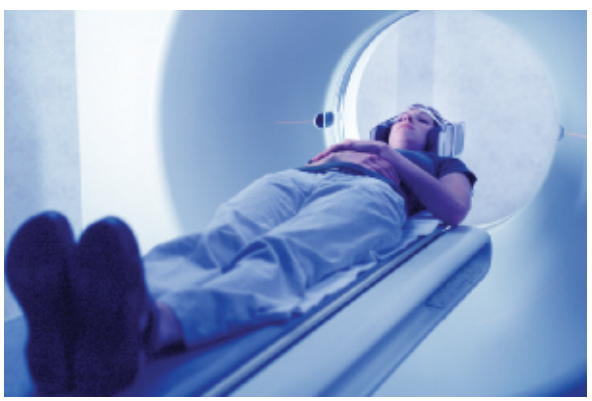
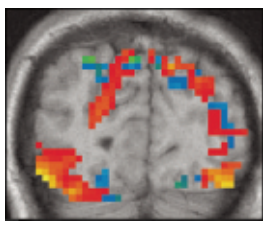


Figure 2.17 Location of the superior temporal sulcus (STS) in the temporal lobe, where the "voice area" of the brain resides according to a modular view of speech perception.

The fact that a specific function—in this case, voice perception—was able to be mapped onto a specific area of the brain in this fMRI study supports a modular view of representation. Throughout this book, we will see many more examples of modularity in the brain in other senses. For instance, in Chapter 5, we'll discuss fMRI research suggesting that there are specific brain areas for perceiving faces versus other objects. But we'll also see how representation in the brain often goes beyond individual modules. As we will see next, specific perceptions are often associated with networks of brain areas that are distributed across the cortex.



(a)



(b)

Figure 2.16 (a) A person in a brain scanner. (b) fMRI record. Each small square represents a voxel, and the colors indicate whether brain activity increased or decreased in each voxel. Red and yellow indicate increases in brain activity; blue and green indicate decreases.

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Distributed Representation

Thinking about the brain in terms of modularity is still discussed today (Kanwisher, 2010). But starting in the late 1900s, researchers also began considering how multiple brain areas work together. One such researcher is computer scientist Geoffrey Hinton, who, along with his colleagues James McClelland and David Rumelhart, proposed that the brain represents information in patterns distributed across the cortex, rather than in one single brain area—a concept known as **distributed representation** (Hinton et al., 1986). A distributed approach to representation focuses on the activity in multiple brain areas and the connections between those areas. Hinton's lifelong work on distributed representation, as modeled by computer programs, won him a Turing Award (also known as the "Nobel Prize of Computing") in 2018, which speaks to the importance of this view of representation.

One example of distributed representation is how the brain responds to pain. When you experience a painful stimulus, like accidentally touching a hot stove, your perception involves multiple components. You might simultaneously experience the sensory component ("it feels burning hot"), an emotional component ("it's unpleasant"), and a reflexive motor component (pulling your hand away). These different aspects of pain activate a number of structures distributed across the brain (**Figure 2.18**). Thus, pain presents a good example of how a single stimulus can cause widespread activity.

Another example of distributed representation is shown in **Figure 2.19**. **Figure 2.19a** shows that the *maximum* activity for houses, faces, and chairs occurs in separate areas in the cortex. This finding is consistent with the idea that there are areas specialized for specific stimuli. If, however, we look at **Figure 2.19b**, which shows *all* of the activity for each type of stimulus, we see that houses, faces, and chairs also cause activity over a wide area of the cortex (Ishai et al., 1999; 2000). We'll discuss modular and distributed representation of objects further in Chapter 5.

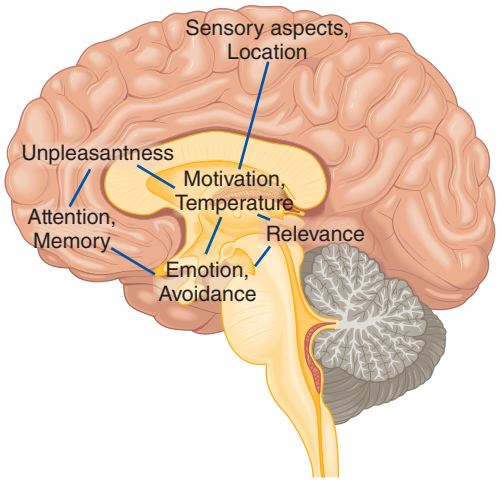

Figure 2.18 Areas that are involved in the perception of pain. Each area serves a different aspect of pain perception.

Connections Between Brain Areas

We've seen how a given perceptual experience can involve multiple brain areas. But what about the connections between those areas? Recent research has shown that connections between brain areas may be just as important for perception as the activity in each of those areas alone (Sporns, 2014).

There are two different approaches to exploring the connections between brain areas. **Structural connectivity** is the "road map" of fibers connecting different areas of the brain. **Functional connectivity** is the neural activity associated

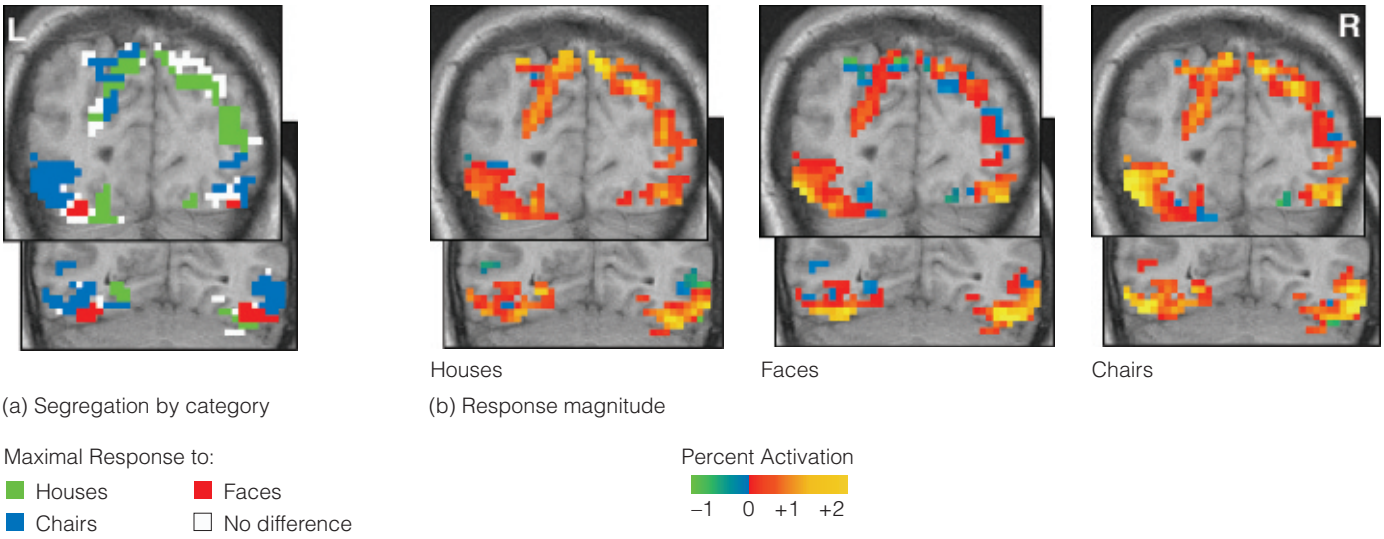

Figure 2.19 fMRI responses of the human brain to houses, faces, and chairs. (a) Areas activated most strongly by each type of stimulus; (b) all areas activated by each type of stimulus, showing that each type of stimulus activates multiple areas. (From Ishai et al., 2000)

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with a particular function that is flowing through this structural network. The distinction between structural and functional connectivity is similar to the one we described in "Method: Brain Imaging," where the *structure* of the brain is measured using magnetic resonance imaging (MRI) and the *functioning* of the brain is measured by functional magnetic resonance imaging (fMRI).

Here's another way to think about structural and functional connectivity. Picture the road network of a large city. On one set of roads, cars are streaming toward the shopping area just outside the city, while on other roads cars are traveling toward the city's business and financial district. One group of people is using roads to reach places to shop; another group is using roads to get to work or conduct business. Thus, the road map is analogous to the brain's structural pathways and connections, and the different traffic patterns are analogous to the brain's functional connectivity. Just as different parts of the city's road network are involved in achieving different goals, so different parts of the brain's neural network are involved in carrying out different cognitive or motor goals.

One way of measuring functional connectivity involves using fMRI to measure resting state activity of the brain. To understand what this means, let's return to the "Brain Imaging" method on page 31. That method described the fMRI measured as a person is engaged in a specific task, such as listening to certain sounds. This type of fMRI is called **task-related fMRI**. It is also possible to record fMRI when the brain is not involved in a specific task. This fMRI is called the **resting-state fMRI**. Resting-state fMRI is used to measure functional connectivity, as follows:

METHOD | The Resting State Method of Measuring Functional Connectivity

Resting-state functional connectivity is measured as follows:

1. Use task-related fMRI to determine a brain location associated with carrying out a specific task. For example, movement of the finger causes an fMRI response at the location marked *Motor (L)* in **Figure 2.20a**. This location is called the seed location.
2. Measure the resting-state fMRI at the seed location. The resting-state fMRI of the seed location, shown in **Figure 2.20b**, is called a time-series response because it indicates how the response changes over time.
3. Measure the resting-state fMRI at another location, which is called the test location. The response of the test location *Somatosensory*, which is located in an area of the brain responsible for sensing touch, is shown in **Figure 2.20c**.
4. Calculate the correlation between the seed and test location responses. The correlation is calculated using a complex mathematical procedure that compares the seed and test responses at a large number of places along the horizontal time axis. **Figure 2.21a** shows the response at the *Somatosensory* test location superimposed on the seed response. The correspondence between these responses results in a high correlation, which indicates high functional connectivity. **Figure 2.21b** shows the seed response and the response at another test location. The poor match between these two responses results in a low correlation, which indicates poor or no functional connectivity.

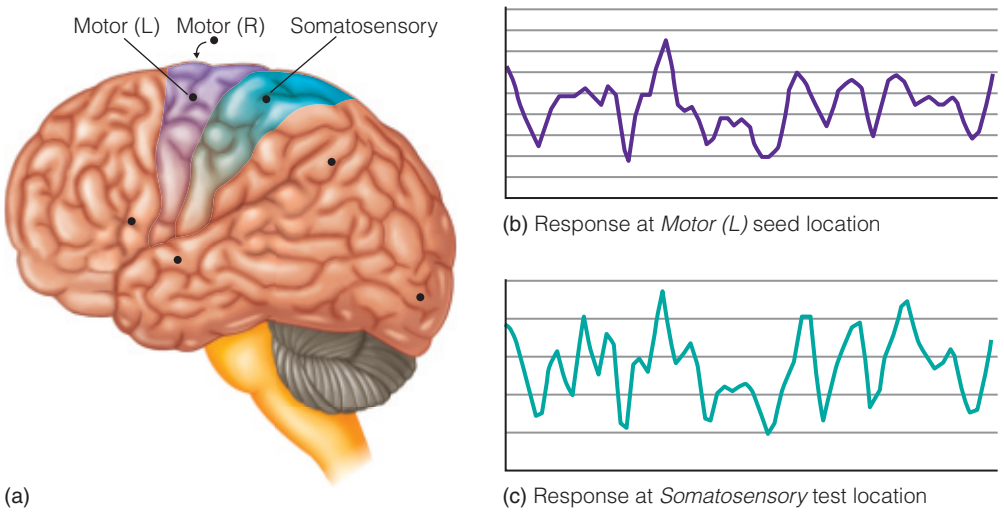

Figure 2.20 How functional connectivity is determined by the resting-state fMRI method. (a) Left hemisphere of the brain, showing the seed location *Motor (L)* in the left motor cortex, and a number of test locations, each indicated by a dot. Test location *Motor (R)* is in the right motor cortex on the other side of the brain from *Motor (L)*. Test location *Somatosensory* is in the *somatosensory* cortex, which is involved in perceiving touch. (b) Resting level fMRI response of the *Motor (L)* seed location. (c) Resting level fMRI response of the *Somatosensory* test location. The responses in (b) and (c) are 4 seconds long. (Responses courtesy of Ying-Hui Chou)

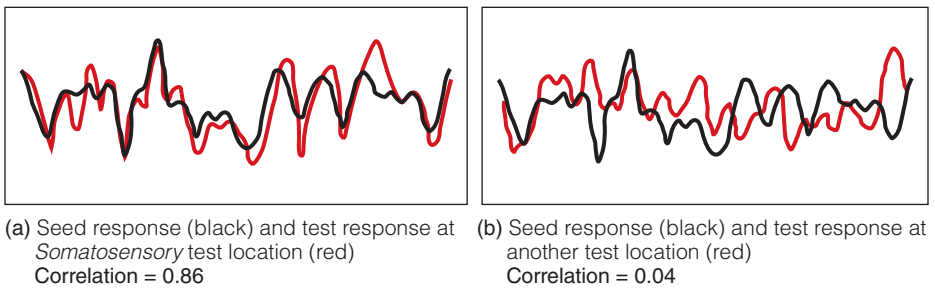
(a) Seed response (black) and test response at *Somatosensory* test location (red)
Correlation = 0.86
(b) Seed response (black) and test response at another test location (red)
Correlation = 0.04

Figure 2.21 Superimposed seed response (black) and test-location response (red). (a) Response of the *Somatosensory* test location, which is highly correlated with the seed response (correlation = 0.86). (b) Response of another test location, which is poorly correlated with the seed response (correlation = 0.04). (Responses courtesy of Yin-Hui Chou)

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Figure 2.22 shows the time-series for the seed location and a number of test locations, and the correlations between the seed and test locations. The test locations *Somatosensory* and *Motor R* are highly correlated with the seed response and so have high functional connectivity with the seed location. This is evidence that these structures are part of a functional network. All of the other locations have low correlations so are not part of the network.

Resting-state functional connectivity is one of the main methods for determining functional connectivity, but there are also other methods. For example, functional connectivity can be determined by measuring the task-related fMRI at the seed and test locations and determining the correlations between the two responses.

It is important to note that saying two areas are functionally connected does not necessarily mean that they directly communicate by neural pathways. For example, the response from two areas can be highly correlated because they are both receiving inputs from another area. Functional connectivity and structural connectivity are not, therefore, the same thing, but they are related, so regions with high structural connectivity often show a high level of functional connectivity (van den Heuvel & Pol, 2010).

So why does it matter if certain brain areas are functionally connected? What does this really tell us about perception? One example of how functional connectivity can help us understand perception is that it can be used to predict behavior. A recent experiment by Sepideh Sadaghiani and coworkers (2015) explored this by using fMRI to look at moment-to-moment functional connectivity across a network of brain areas. The participants' task was to detect a very quiet sound that was only perceptible 50 percent of the time—in other words, it was at the participant's *detection threshold* (see Chapter 1, page 14). The researchers found that the strength of functional connectivity immediately *before* the detection task predicted how likely it was that the person would hear the sound. So, the person was more likely to report hearing the sound when their neural connections were stronger. Other research has observed similar effects in other senses. For example, a person's resting-state functional connectivity can predict whether or not they will perceive a hot stimulus on their foot as painful (Ploner et al., 2010).

By examining the structural and functional connectivity between brain areas in a network, in addition to the activation in each brain area alone, researchers can get a more comprehensive picture of how the brain represents our perceptual experiences.

SOMETHING TO CONSIDER:

The Mind–Body Problem

The main goal of our discussion so far has been to explore the electrical signals that are the link between the environment and our perception of the environment. The idea that nerve impulses can represent things in the environment is what is

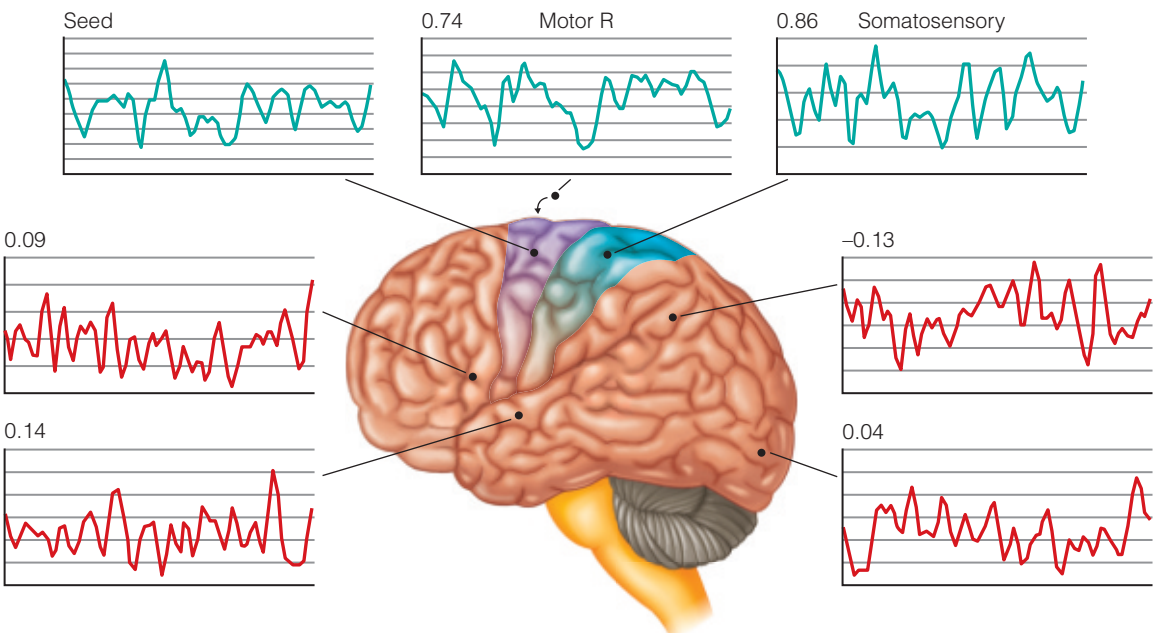

Figure 2.22 Resting-state fMRI responses for the *Motor (L)* seed, test locations *Motor (R)*, *Somatosensory*, and five test locations in other parts of the brain. The numbers indicate correlations between the seed response and each test-location response. Responses *Motor (R)* and *Somatosensory* have been singled out because they have high correlations, which indicates high functional connectivity with the seed. The other locations have low correlations so are not functionally connected to the seed location. (Responses courtesy of Yin-Hui Chou)

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behind the following statement, written by Bernita Rabinovitz, a student in my class.

> A human perceives a stimulus (a sound, a taste, etc.). This is explained by the electrical impulses sent to the brain. This is so incomprehensible, so amazing. How can one electrical impulse be perceived as the taste of a sour lemon, another impulse as a jumble of brilliant blues and greens and reds, and still another as bitter, cold wind? Can our whole complex range of sensations be explained by just the electrical impulses stimulating the brain? How can all of these varied and very concrete sensations—the ranges of perceptions of heat and cold, colors, sounds, fragrances and tastes—be merely and so abstractly explained by differing electrical impulses?

When Bernita asks how hot and cold, colors, sounds, fragrances, and tastes can be explained by electrical impulses, she is asking about the **mind–body problem**: How do physical processes like nerve impulses (the body part of the problem) become transformed into the richness of perceptual experience (the mind part of the problem)?

As we continue on to discuss vision in the following chapters, and the other senses later in this book, we'll see many examples of the connections between electrical signals in the nervous system and what we perceive. We will see that when we look out at a scene, countless neurons are firing—some to the basic features of a stimulus (discussed in Chapter 4), and others to entire objects, like faces or bodies (discussed in Chapter 5).

You may think that all of these connections between electrical signals and perception provide a solution to the mind–body problem. This is not, however, the case, because as impressive as these connections are, they are all just *correlations*—demonstrations of *relationships* between neural firing and perception (**Figure 2.23a**). But the mind–body problem goes beyond asking how physiological responses *correlate* with perception. It asks how physiological processes *cause* our experience. Think about what this means. The mind–body problem is asking how the flow of sodium and potassium ions across membranes that creates nerve impulses becomes *transformed* into the experience we have when we see a friend's face or when we experience the color of a red rose (**Figure 2.23b**). Just showing that a neuron *fires* to a face or the color red doesn't answer the question of how the firing *creates* the experience of seeing a face or perceiving the color red.

Thus, the physiological research we describe in this book, although extremely important for understanding the physiological mechanisms responsible for perception, does not provide a solution to the mind–body problem. Researchers (Baars, 2001; Crick & Koch, 2003) and philosophers (Block, 2009) may discuss the mind–body problem, but when researchers step into the laboratory, their efforts are devoted to doing experiments like the ones we have discussed so far, which search for correlations between physiological responses and experience.

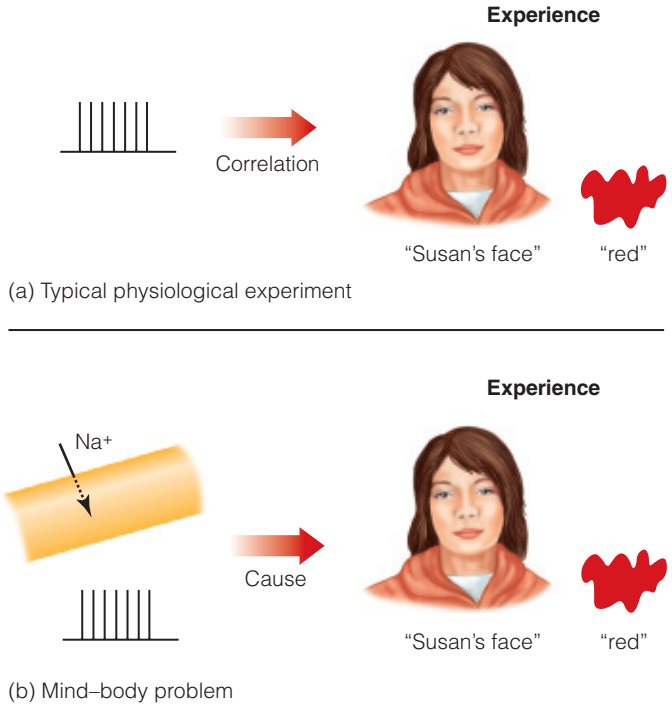

Figure 2.23 (a) This illustrates the situation for most of the physiological experiments we will be describing in this book, which determine correlations between physiological responding such as nerve firing and experiences such as perceiving "Susan's face" or "red." (b) Solving the mind–body problem requires going beyond demonstrating correlations to determine how ion flow or nerve firing causes the experiences of "Susan's face" or the color "red."

TEST YOURSELF 2.2

1. What is phrenology, and what insight did it provide into neural representation?
2. Explain how neuropsychological case studies can support a modular view of neural representation, using Broca's research as an example.
3. Describe the technique of brain imaging. How can fMRI be used to study modularity?
4. What is distributed representation? Provide an example from one of the senses.
5. Discuss the difference between structural and functional connectivity. Which technique might be used if one was interested in studying the neural connections associated with a certain task, and why?
6. Describe how functional connectivity is determined. What is the resting-state method?
7. How can functional connectivity provide insight into perception?
8. What is the mind–body problem? Why do we say that demonstrating connections between nerve firing and a particular stimulus like a face or a color does not solve the mind–body problem?

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THINK ABOUT IT

1. Because the long axons of neurons look like electrical wires, and both neurons and electrical wires conduct electricity, it is tempting to equate the two. Compare the functioning of axons and electrical wires in terms of their structure and the nature of the electrical signal they conduct.
2. We described pain as consisting of multiple components. Can you think of ways that other objects or experiences consist of multiple components? If you can, what does that say about the neural representation of these objects or experiences?

KEY TERMS

Action potential (p. 22)
Axon (p. 22)
Brain imaging (p. 31)
Broca's area (p. 31)
Cell body (p. 21)
Dendrites (p. 22)
Depolarization (p. 24)
Distributed representation (p. 33)
Excitatory response (p. 26)
Falling phase of the action potential (p. 25)
Functional connectivity (p. 33)
Functional magnetic resonance imaging (fMRI) (p. 31)
Grandmother cell (p. 27)
Hyperpolarization (p. 25)
Inhibitory response (p. 26)
Ions (p. 24)
Magnetic resonance imaging (MRI) (p. 31)
Mind–body problem (p. 36)
Modularity (p. 31)
Module (p. 31)
Nerve fiber (p. 22)
Neurons (p. 21)
Neuropsychology (p. 31)
Neurotransmitters (p. 26)
Permeability (p. 24)
Phrenology (p. 30)
Population coding (p. 29)
Propagated response (p. 23)
Receptor sites (p. 26)
Refractory period (p. 24)
Resting potential (p. 22)
Resting-state fMRI (p. 34)
Resting-state functional connectivity (p. 34)
Rising phase of the action potential (p. 24)
Seed location (p. 34)
Sensory coding (p. 27)
Sparse coding (p. 29)
Specificity coding (p. 27)
Spontaneous activity (p. 24)
Structural connectivity (p. 33)
Synapse (p. 25)
Task-related fMRI (p. 34)
Test location (p. 34)
Wernicke's area (p. 31)

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One message of this book is that perceptual experience is shaped by properties of the perceptual system. The sharp, colorful scene represents perception created by activation of cone receptors in the retina. The less focused, grey-scale scene represents perception created by activation of rod receptors in the retina.

Bruce Goldstein

Learning Objectives

After studying this chapter, you will be able to …

- Identify the key structures of the eye and describe how they work together to focus light on the retina.
- Explain how light is transduced into an electrical signal.
- Distinguish between the influence of rods and cones on perception in both dark and light environments.
- Use your knowledge of neural processing to explain how signals travel through the retina.
- Describe how lateral inhibition and convergence underlie center-surround antagonism in ganglion cell receptive fields.
- Understand the development of visual acuity over the first year of life.

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CHAPTER 3

The Eye and Retina

CHAPTER CONTENTS

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Light: The Stimulus for Vision
The Eye
DEMONSTRATION: Becoming Aware of the Blind Spot
DEMONSTRATION: Filling in the Blind Spot
3.2 Focusing Light Onto the Retina
Accommodation
DEMONSTRATION: Becoming Aware of What Is in Focus
Refractive Errors
3.3 Photoreceptor Processes
Transforming Light Energy Into Electrical Energy
Adapting to the Dark
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Spectral Sensitivity
METHOD: Measuring a Spectral Sensitivity Curve
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Ganglion Cell Receptive Fields
SOMETHING TO CONSIDER: Early Events Are Powerful
DEVELOPMENTAL DIMENSION: Infant Visual Acuity
METHOD: Preferential Looking
TEST YOURSELF 3.2
THINK ABOUT IT

Some Questions We Will Consider:

- How does the focusing system at the front of our eye affect our perception? (p. 43)
- How do chemicals in the eye called visual pigments affect our perception? (p. 45)
- How can the way neurons are "wired up" in the retina affect perception? (p. 51)

We begin with the story of Larry Hester—a retired tire salesman from North Carolina. In his early 30s, Larry began noticing a rapid decline in his vision. He had always had poor eyesight, but this was different; it almost looked like the world was closing in on him. Upon seeing an ophthalmologist, Larry was given the shocking news that he had a genetic disorder of the eye called *retinitis pigmentosa* that would result in total blindness, and that there was no stopping it (Graham, 2017).

Larry lost his vision and was left in complete darkness for the next 33 years. But then something amazing happened: He had the opportunity to have some of his vision restored. Larry was a candidate for a new technology referred to as the bionic eye—an array of electrodes implanted in the back of the eye that, through a camera mounted on eyeglasses, sends signals to the visual system about what is "out there" in the world (Da Cruz et al., 2013; Humayun et al., 2016). While the bionic eye doesn't completely restore vision, it allows the person to see contrasting lightness versus darkness, such the edge between where one object ends and another begins—a concept we'll return to later in this chapter. This might not seem very impressive to someone with normal vision, but to Larry, who couldn't see anything for half of his life, suddenly being able to see the lines in the crosswalk or the edges of his wife's face was monumental. It meant that he could use vision to interact with his world again. As Larry once described in an interview, "Light is so basic and probably wouldn't have significance to anybody else, but to me, it means I can see."

Larry's story demonstrates the importance of light, the eyes, and the cells at the back of the eyes. A great deal of processing takes place within the eyes. This chapter focuses on these processes and marks the beginning of our journey into the sense of vision. After we discuss the early stages of the visual perceptual process in this chapter, Chapter 4 will go on to discuss the later stages of processing that occur when the signals leave the eye and reach the brain. Then, Chapters 5–10 will

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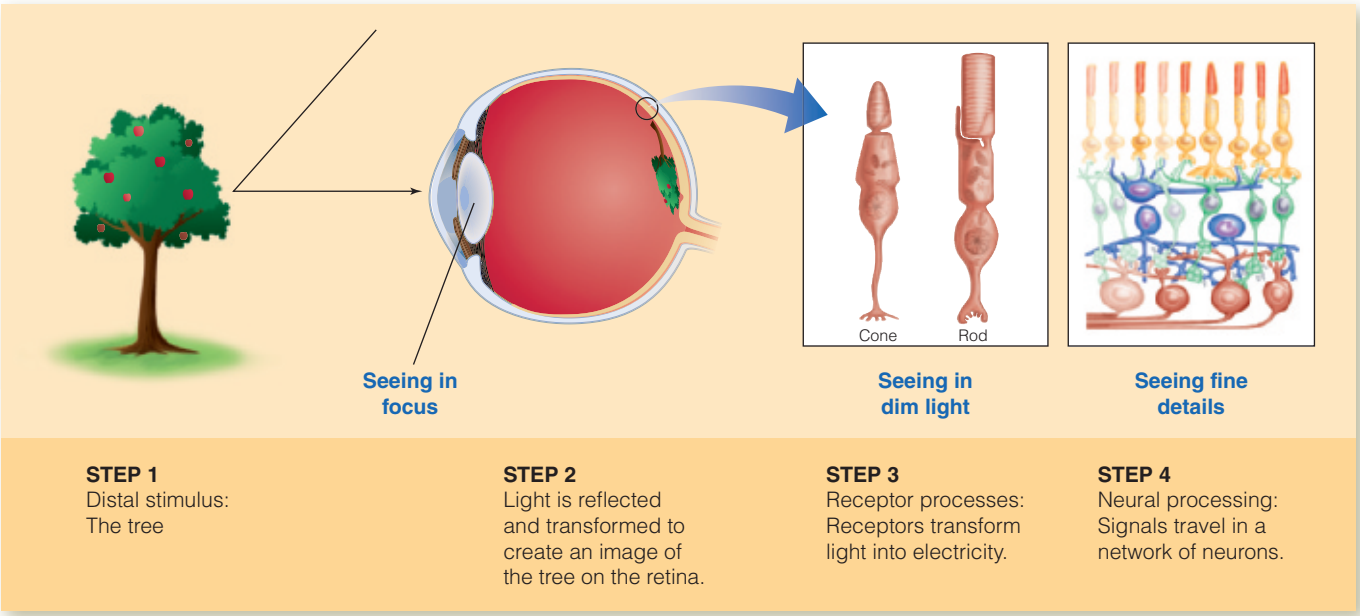
Cone
Rod
Seeing in focus
Seeing in dim light
Seeing fine details
STEP 1
Distal stimulus: The tree
STEP 2
Light is reflected and transformed to create an image of the tree on the retina.
STEP 3
Receptor processes: Receptors transform light into electricity.
STEP 4
Neural processing: Signals travel in a network of neurons.

Figure 3.1 Chapter preview. This chapter will describe the first three steps of the perceptual process for vision and will introduce step 4. Physical processes for each step are indicated along the bottom; the perceptual outcomes of these processes are indicated in blue.

discuss more specific aspects of vision, such as how we perceive objects, motion, and color.

Figure 3.1 shows the first four steps of the visual process. Following the sequence of the physical events in the process, shown in black along the bottom of the figure, we begin with Step 1, the distal stimulus (the tree); then move to Step 2, in which light is reflected from the tree and enters the eye to create the proximal stimulus on the visual receptors; then to Step 3, in which receptors transform light into electrical signals; and finally to Step 4, in which electrical signals are "processed" as they travel through a network of neurons. Our goal in this chapter is to show how these physical events influence the following aspects of perception, shown in blue in Figure 3.1: (1) seeing in focus, (2) seeing in dim light, and (3) seeing fine details. We begin by describing light, the eye, and the receptors in the retina that line the back of the eye.

3.1 Light, the Eye, and the Visual Receptors

The ability to see a tree, or any other object, depends on light being reflected from that object into the eye.

Light: The Stimulus for Vision

Vision is based on visible light, which is a band of energy within the electromagnetic spectrum. The electromagnetic spectrum is a continuum of electromagnetic energy that is produced by electric charges and is radiated as waves (see Figure 1.23, page 18). The energy in this spectrum can be described by its wavelength—the distance between the peaks of the electromagnetic waves. The wavelengths in the electromagnetic spectrum range from extremely short-wavelength gamma rays (wavelength = about 10^{-12} meters, or one ten-billionth of a meter) to long-wavelength radio waves (wavelength = about 10^{4} meters, or 10,000 meters).

Visible light, the energy within the electromagnetic spectrum that humans can perceive, has wavelengths ranging from about 400 to 700 nanometers (nm), where 1 nanometer = 10^{-9} meters, which means that the longest visible wavelengths are slightly less than one-thousandth of a millimeter long. For humans and some other animals, the wavelength of visible light is associated with the different colors of the spectrum, with short wavelengths appearing blue, middle wavelengths green, and long wavelengths yellow, orange, and red.

The Eye

The eyes contain the receptors for vision. The first eyes, which appeared back in the Cambrian period (570–500 million years ago), were eyespots on primitive animals such as flatworms that could distinguish light from dark but couldn't detect features of the environment. Detecting an object's details didn't become possible until more sophisticated eyes evolved to include optical systems that could produce images and therefore provide information about shapes and details of objects and the arrangement of objects within scenes (Fernald, 2006).

Light reflected from objects in the environment enters the eye through the pupil and is focused by the cornea and lens to form sharp images of the objects on the retina, the network of neurons that covers the back of the eye and that contains the receptors for vision, also known as photoreceptors (**Figure 3.2a**). There are two types of photoreceptors, rods and

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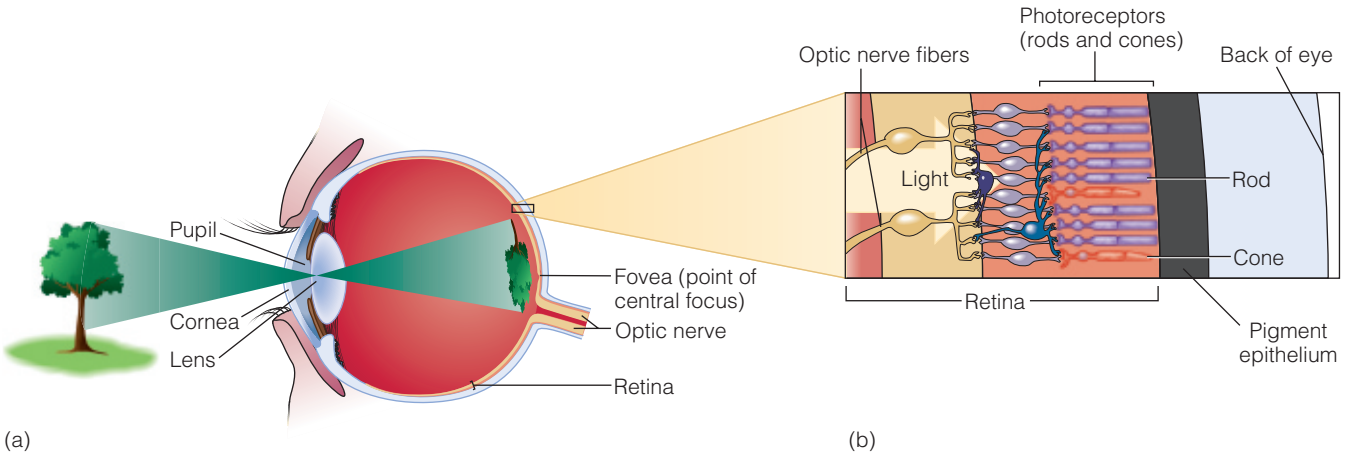

Figure 3.2 An image of the tree is focused on the retina, which lines the back of the eye. The close-up of the retina on the right shows the receptors and other neurons that make up the retina.

cones, so called because of the rod- and cone-shaped **outer segments** (**Figure 3.3**). The outer segments are the part of the receptor that contains light-sensitive chemicals called **visual pigments** that react to light and trigger electrical signals. Signals from the receptors flow through the network of neurons that make up the retina (**Figure 3.2b**) and emerge from the back of the eye in the **optic nerve**, which contains a million optic nerve fibers that conduct signals toward the brain.

The rod and cone receptors not only have different shapes, they are also distributed differently across the retina. From **Figure 3.4**, which indicates the rod and cone distributions, we can conclude the following:

1. One small area, the **fovea**, contains only cones. When we look directly at an object, the object's image falls on the fovea.
2. The **peripheral retina**, which includes all of the retina outside of the fovea, contains both rods and cones. It is important to note that although the fovea has *only* cones, there are also many cones in the peripheral retina. The fovea is so small (about the size of this "o") that it contains only about 1 percent, or 50,000, of the 6 million cones in the retina (Tyler, 1997a, 1997b).
3. The peripheral retina contains many more rods than cones because there are about 120 million rods and only 6 million cones in the retina.

One way to appreciate the fact that the rods and cones are distributed differently in the retina is by considering what happens when functioning receptors are missing from one area of the retina. A condition called **macular degeneration**, which is most common in older people, destroys the cone-rich fovea and a small area that surrounds it. (*Macula* is a term usually associated with medical practice that includes the fovea plus a small area surrounding the fovea.) This creates a blind region in central vision, so when a person looks directly at something, he or she loses sight of it (**Figure 3.5a**).

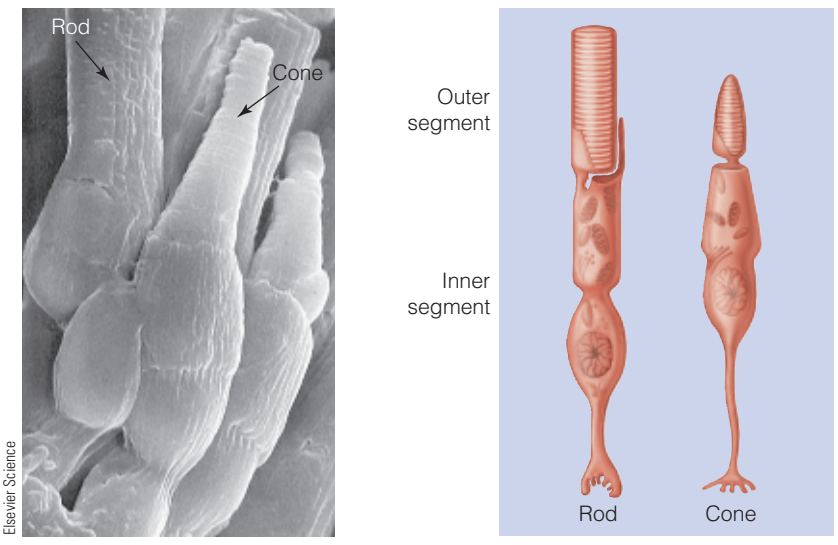

Figure 3.3 (a) Scanning electromicrograph of the rod and cone receptors in the retina, showing the rod-shaped and cone-shaped receptor outer segments. (b) Rod and cone receptors, showing the inner and outer segments. The outer segments contain the light-sensitive visual pigment. (From Lewis et al., 1969)

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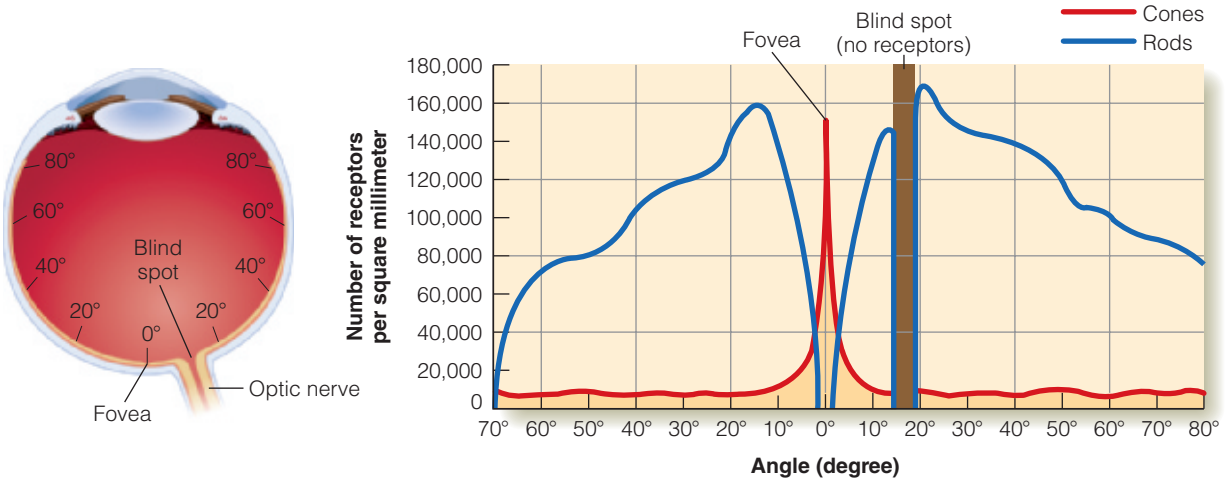
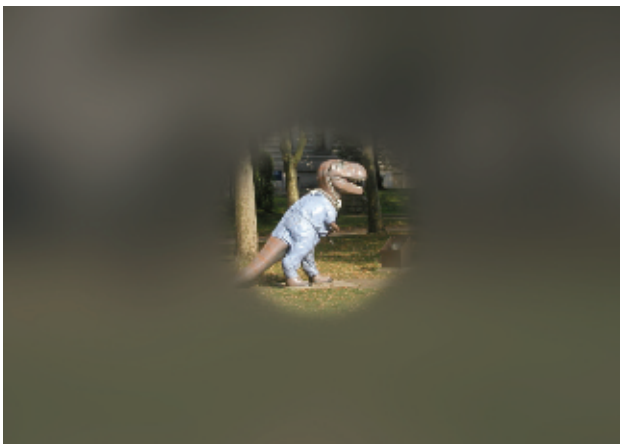


Figure 3.4 The distribution of rods and cones in the retina. The eye on the left indicates locations in degrees relative to the fovea. These locations are repeated along the bottom of the chart on the right. The vertical brown bar near 20 degrees indicates the place on the retina where there are no receptors because this is where the ganglion cells leave the eye to form the optic nerve. (Adapted from Lindsay & Norman, 1977)

(a)



(b)

Figure 3.5 (a) In a condition called macular degeneration, the fovea and surrounding area degenerate, so the person cannot see whatever he or she is looking at. (b) In retinitis pigmentosa, the peripheral retina initially degenerates and causes loss of vision in the periphery. The resulting condition is sometimes called "tunnel vision."

Another condition, **retinitis pigmentosa**, which led to Larry Hester's blindness, is a degeneration of the retina that is passed from one generation to the next (although not always affecting everyone in a family). This condition first attacks the peripheral rod receptors and results in poor vision in the peripheral visual field (**Figure 3.5b**). Eventually, in severe cases, the foveal cone receptors are also attacked, resulting in complete blindness.

Before leaving the rod–cone distribution shown in Figure 3.4, note that there is one area in the retina, indicated by the vertical brown bar, where there are no photoreceptors. **Figure 3.6** shows a close-up of the place where this occurs, which is where the nerve fibers that make up the optic nerve leave the eye. Because of the absence of photoreceptors, this place is called the **blind spot**. Although

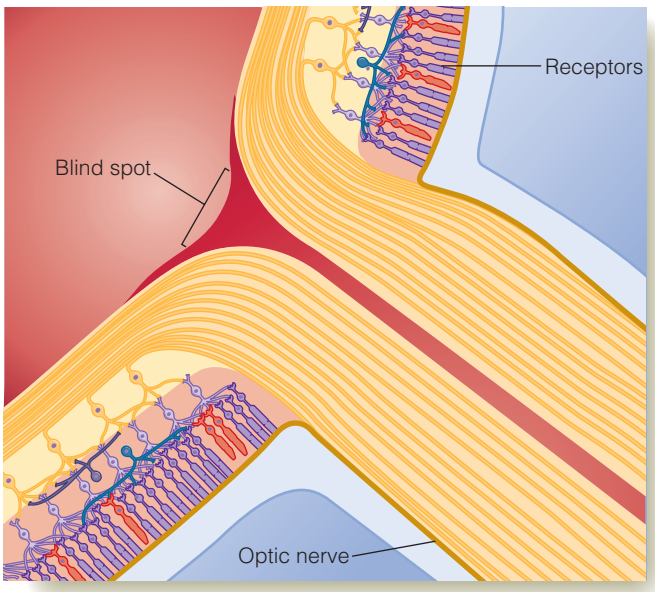


Figure 3.6 There are no receptors at the place where the optic nerve leaves the eye. This enables the receptors' ganglion cell fibers to flow into the optic nerve. The absence of receptors in this area creates the blind spot.

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you are not normally aware of the blind spot, you can become aware of it by doing the following demonstration.

DEMONSTRATION | Becoming Aware of the Blind Spot

Place the book (or your electronic device if you are reading the ebook) on your desk. Close your right eye, and position yourself above the book/device so that the cross in **Figure 3.7** is aligned with your left eye. Be sure the book page is flat and, while looking at the cross, slowly move closer. As you move closer, be sure not to move your eye from the cross, but at the same time keep noticing the circle off to the side. At some point, around 3 to 9 inches from the book/device, the circle should disappear. When this happens, the image of the circle is falling on your blind spot.

Figure 3.7 Blind spot demonstration.

Why aren't we usually aware of the blind spot? One reason is that the blind spot is located off to the side of our visual field, where objects are not in sharp focus. Because of this and because we don't know exactly where to look for it (as opposed to the demonstration, in which we are focusing our attention on the circle), the blind spot is hard to detect.

But the most important reason that we don't see the blind spot is that a mechanism in the brain "fills in" the place where the image disappears (Churchland & Ramachandran, 1996). The next demonstration illustrates an important property of this filling-in process.

DEMONSTRATION | Filling in the Blind Spot

Close your right eye and, with the cross in **Figure 3.8** lined up with your left eye, move toward the wheel. When the center of the wheel falls on your blind spot, notice how the spokes of the wheel fill in the hole (Ramachandran, 1992).

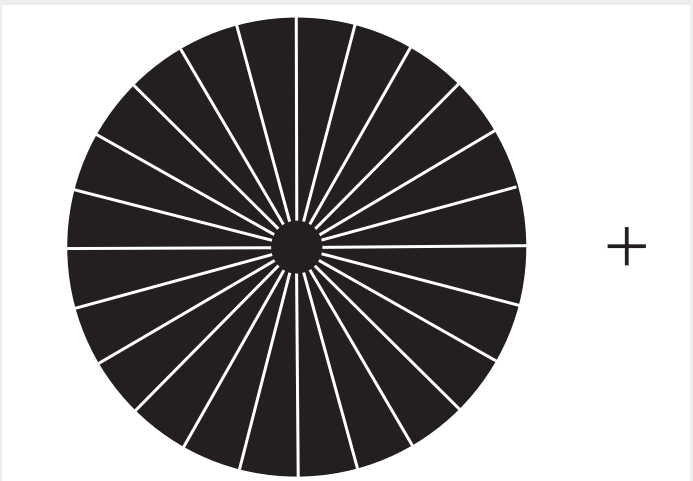

Figure 3.8 View the pattern as described in the text, and observe what happens when the center of the wheel falls on your blind spot.
(Adapted from Ramachandran, 1992)

These demonstrations show that the brain does not fill in the area served by the blind spot with "nothing"; rather, it creates a perception that matches the surrounding pattern—the grey page in the first demonstration, and the spokes of the wheel in the second one. This "filling in" is a preview of one of the themes of the book: how the brain creates a coherent perception of our world. For now, however, we return to the visual process, as light reflected from objects in the environment is focused onto the receptors (step 2 in Figure 3.1).

3.2 Focusing Light Onto the Retina

Light reflected from an object into the eye is focused onto the retina by a two-element optical system: the cornea and the lens (**Figure 3.9a**). The cornea, the transparent covering of the front of the eye, accounts for about 80 percent of the eye's focusing power, but like the lenses in eyeglasses, it is fixed in place so it can't adjust its focus. The lens, which supplies the remaining 20 percent of the eye's focusing power, can change its shape to adjust the eye's focus for objects located at different distances. This change in shape is achieved by the action of *ciliary muscles*, which increase the focusing power of the lens (its ability to bend light) by increasing its curvature (compare **Figure 3.9b** and **Figure 3.9c**).

We can understand why the eye needs to adjust its focus by first considering what happens when the eye is relaxed and a person with normal (20/20) vision views a small object that is far away. If the object is located more than about 20 feet away, the light rays that reach the eye are essentially parallel (Figure 3.9a), and the cornea–lens combination brings these parallel rays to a focus on the retina at point A. But if the object moves closer to the eye, the light rays reflected from this object enter the eye at more of an angle, and this pushes the focus point back so if the back of the eye weren't there, light would be focused at point B (Figure 3.9b). Because the light is stopped by the back of the eye before it reaches point B, the image on the retina is out of focus, so if things remained in this state, the person would see the object as blurred. The adjustable lens, which controls a process called *accommodation*, comes to the rescue to help prevent blurring.

Accommodation

Accommodation is the change in the lens's shape that occurs when the ciliary muscles at the front of the eye tighten and increase the curvature of the lens so that it gets thicker (Figure 3.9c). This increased curvature increases the bending of the light rays passing through the lens so the focus point is pulled from point B back to A to create a sharp image on the retina. This means that as you look around at different objects, your eye is constantly adjusting its focus by accommodating, especially for nearby objects. The following demonstration shows that this is necessary because everything is not in focus at once.

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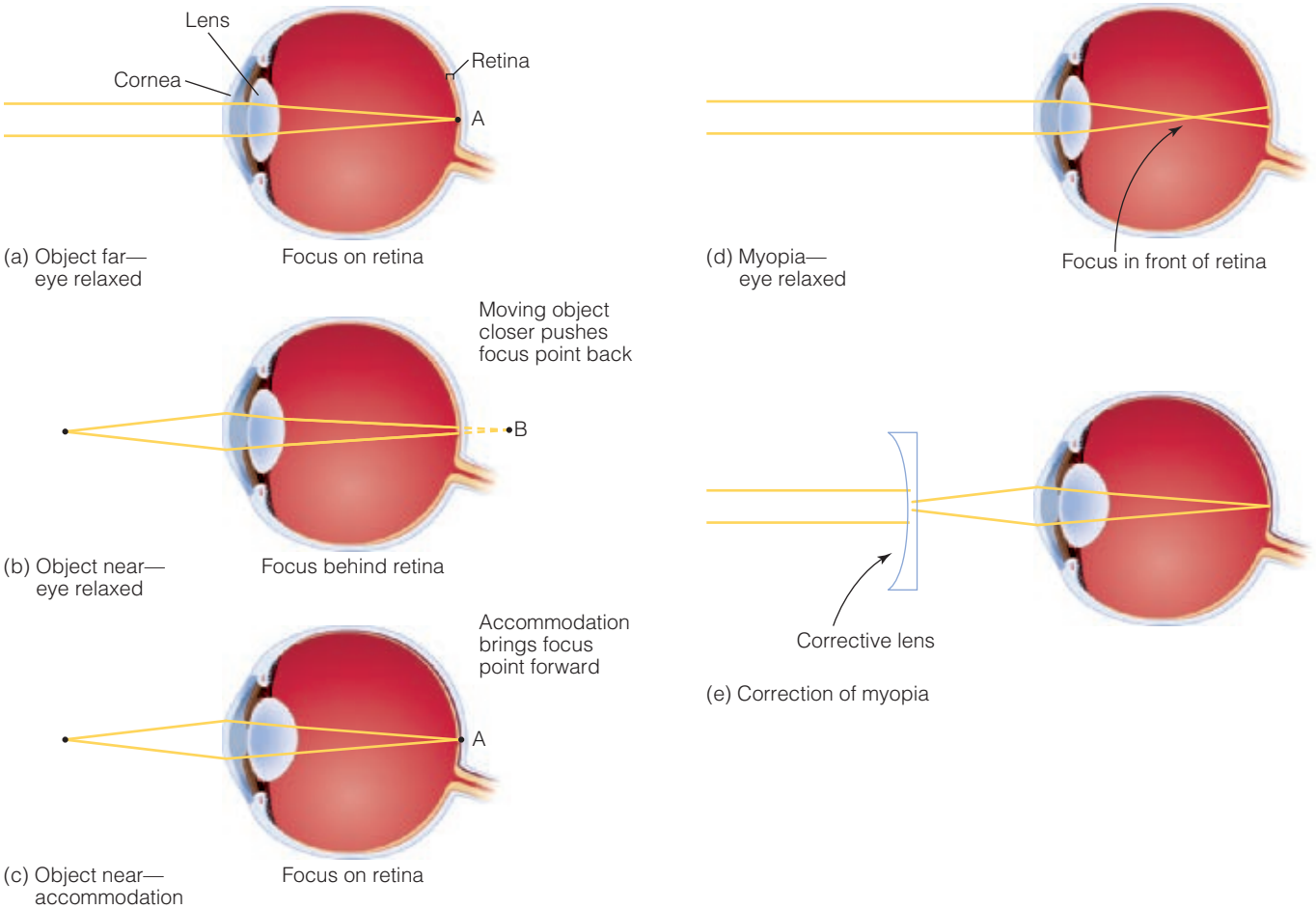

Figure 3.9 Focusing of light rays by the eye. (a) Rays of light coming from a small light source that is more than 20 feet away are approximately parallel. The focus point for parallel light is at A on the retina. (b) Moving an object closer to the relaxed eye pushes the focus point back. Here the focus point is at B, but light is stopped by the back of the eye, so the image on the retina is out of focus. (c) Accommodation of the eye (indicated by the fatter lens) increases the focusing power of the lens and brings the focus point for a near object back to A on the retina, so it is in focus. This accommodation is caused by the action of the ciliary muscles, which are not shown. (d) In the myopic (nearsighted) eye, parallel rays from a distant spot of light are brought to a focus in front of the retina, so distant objects appear blurred. (e) A corrective lens bends light so it is focused on the retina.

DEMONSTRATION | Becoming Aware of What Is in Focus

Accommodation occurs unconsciously, so you are usually unaware that the lens is constantly changing its focusing power to let you see clearly at different distances. This unconscious focusing process works so efficiently that most people assume that everything, near and far, is always in focus. You can demonstrate that this is not so by holding a pen or a pencil, point up, at arm's length, closing one eye, and looking past the pencil at an object that is at least 20 feet away. As you stay focused on the faraway object, notice the pencil point without actually looking at it (be sure to stay focused on the far object). The point will probably appear slightly blurred.

Then slowly move the pencil toward you while still looking at the far object. Notice that as the pencil moves closer, the point becomes more blurred. When the pencil is about 12 inches away, shift your focus to the pencil point. This shift in focus causes the pencil point to appear sharp, but the far object is now out of focus.

When you changed focus from far away to the nearby pencil point during this demonstration, you were changing your accommodation. Either near objects or far objects can be in focus, but not both at the same time. Accommodation, therefore, makes it possible to adjust vision for different distances.

Refractive Errors

While accommodation can help put things into focus, it's not foolproof; sometimes focusing the image onto the retina fails, even with accommodation. There are a number of errors that can affect the ability of the cornea and/or lens to focus the visual input onto the retina. Collectively, these are called **refractive errors**.

The first refractive error that we will discuss often occurs in normal aging. As people get older, their ability to accommodate decreases due to hardening of the lens and weakening of the ciliary muscles, and so they become

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unable to accommodate enough to see objects, or read, at close range. This age-related loss of the ability to accommodate, called **presbyopia** (for "old eye"), can be dealt with by wearing reading glasses, which brings near objects into focus by replacing the focusing power that can no longer be provided by the lens.

Another refractive error that can be solved by a corrective lens is **myopia**, or **nearsightedness**, an inability to see distant objects clearly. The reason for this difficulty, which affects more than 70 million Americans, is illustrated in **Figure 3.9d**. Myopia occurs when the optical system brings parallel rays of light into focus at a point in front of the retina, so the image that reaches the retina is blurred. This problem can be caused by either of two factors: (1) **refractive myopia**, in which the cornea and/or the lens bends the light too much, or (2) **axial myopia**, in which the eyeball is too long. Either way, images of faraway objects are not focused sharply. Corrective lenses can solve this problem, as shown in **Figure 3.9e**.

Finally, people with **hyperopia**, or **farsightedness**, can see distant objects clearly but have trouble seeing nearby objects because the focus point for parallel rays of light is located behind the retina, usually because the eyeball is too short. Young people can bring the image forward onto the retina by accommodating. However, older people, who have difficulty accommodating, often use corrective lenses that bring the focus point forward onto the retina.

Focusing an image clearly onto the retina is the initial step in the process of vision, but although a sharp image on the retina is essential for clear vision, we do not see the image on the retina. Vision occurs not in the retina but in the brain. Before the brain can create vision, the light on the retina must activate the photoreceptors in the retina. This brings us to the next step of the visual process (step 3 in Figure 3.1): processing by the photoreceptors.

3.3 Photoreceptor Processes

Now that we know how light is reflected and focused onto the retina, we next need to understand how the photoreceptors react to that incoming light. As we will see, the light-sensitive visual pigments (see Figure 3.2) play a key role in these photoreceptor processes. In this section, we first describe transduction, and then how the photoreceptors shape perception.

Transforming Light Energy Into Electrical Energy

Transduction is the transformation of one form of energy into another form of energy (see Chapter 1, page 8). Visual transduction occurs in photoreceptors (the rods and cones) and transforms light into electricity. The starting point for understanding how the rods and cones create electricity are the millions of molecules of a light-sensitive visual pigment that are contained in the outer segments of the photoreceptors (Figure 3.3). Visual pigments have two parts: a long protein called *opsin* and a much smaller light-sensitive component called *retinal*. **Figure 3.10a** shows a model of a retinal molecule attached to opsin (Wald, 1968). Note that only a small part of the opsin is shown here; it is actually hundreds of times longer than the retinal. Despite its small size compared to the opsin, retinal is the crucial part of the visual pigment molecule, because when the retinal and opsin are combined, the resulting molecule absorbs visible light.

When incoming light hits the retina, the first step of transduction is initiated: the visual pigment molecule absorbs the light. This causes the retinal within that molecule to change its shape, from being bent, as shown in Figure 3.10a, to straight, as shown in **Figure 3.10b**. This change of shape, called

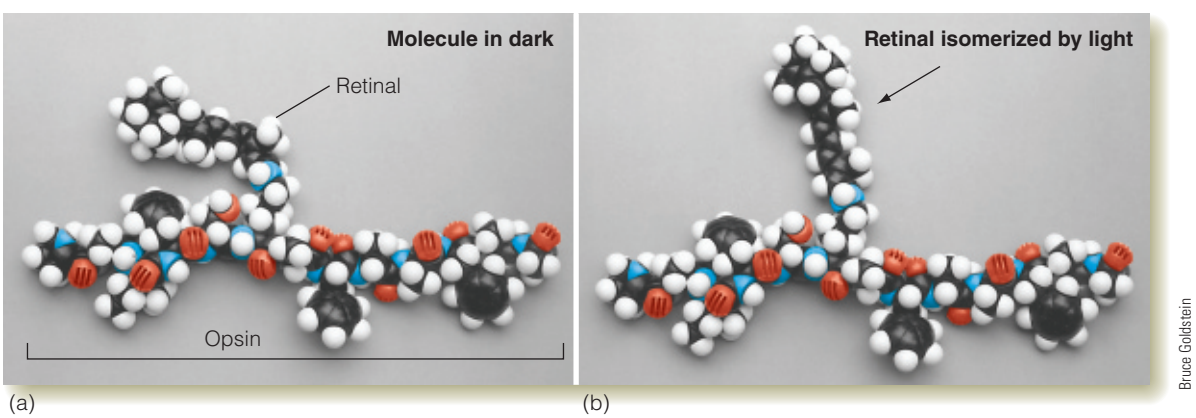

Figure 3.10 Model of a visual pigment molecule. The horizontal part of the model shows a tiny portion of the huge opsin molecule near where the retinal is attached. The smaller molecule on top of the opsin is the light-sensitive retinal. (a) The retinal molecule's shape before it absorbs light. (b) The retinal molecule's shape after it absorbs light. This change in shape, which is called isomerization, triggers a sequence of reactions that culminates in generation of an electrical response in the receptor.

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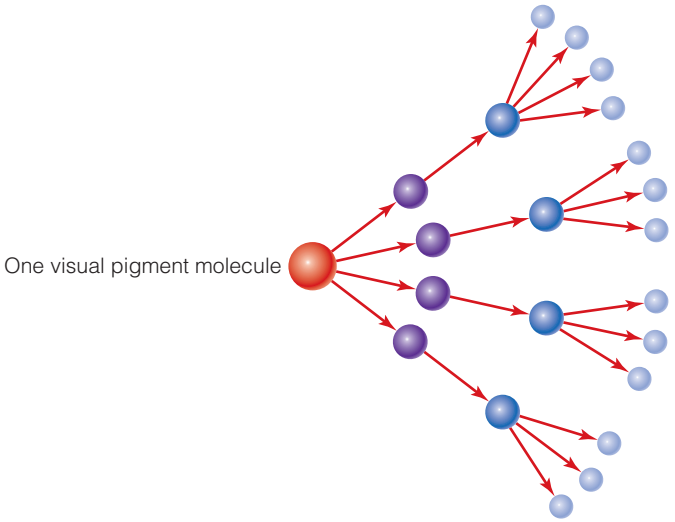

Figure 3.11 This sequence symbolizes the chain reaction that is triggered when a single visual pigment molecule is isomerized by absorption of light. In the actual sequence of events, each visual pigment molecule activates hundreds more molecules, which, in turn, each activate about a thousand molecules. Isomerization of just one visual pigment molecule activates about a million other molecules, which activates the receptor.

isomerization, creates a chemical chain reaction, illustrated in **Figure 3.11**, that activates thousands of charged molecules to create electrical signals in receptors (Baylor, 1992; Hamer et al., 2005). Through this amplification, the initial isomerization of just one visual pigment molecule can ultimately lead to activation of the entire photoreceptor. An electrical signal has now been created, which means that transduction is complete.

Next, we will demonstrate how properties of the visual pigments influence perception. We do this by comparing the perceptions caused by the rod and cone photoreceptors. As we will see, the visual pigments in these two types of photoreceptors influence two aspects of visual perception: (1) how we adjust to darkness, and (2) how well we see light in different parts of the spectrum.

Adapting to the Dark

When we discussed measuring perception in Chapter 1, we noted that when a person goes from a lighted environment to a dark place, it may be difficult to see at first, but that after some time in the dark, the person becomes able to make out lights and objects that were invisible before (Figure 1.18, page 16). This process of increasing sensitivity in the dark, called dark adaptation, is measured by determining a dark adaptation curve. In this section we will show how the rod and cone receptors control an important aspect of vision: the ability of the visual system to adjust to dim levels of illumination. We will describe how the dark adaptation curve is measured, and how the increase in sensitivity that occurs in the dark has been linked to properties of the rod and cone visual pigments.

Measuring the Dark Adaptation Curve The study of dark adaptation begins with measuring the dark adaptation curve, which is the function relating sensitivity to light to time in the dark, beginning when the lights are extinguished.

METHOD | Measuring the Dark Adaptation Curve

The first step in measuring a dark adaption curve is to have the participant look at a small fixation point while paying attention to a flashing test light that is off to the side (**Figure 3.12**). Because the participant is looking directly at the fixation point, its image falls on the fovea, so the image of the test light, which is off to the side, falls on the peripheral retina, which contains both rods and cones. While still in the light, the participant turns a knob that adjusts the intensity of the flashing light until it can just barely be seen (this is the *method of adjustment* introduced in Chapter 1). This threshold for seeing the light, the minimum amount of energy necessary to just barely see the light, is then converted to *sensitivity*. Because sensitivity = 1/threshold, this means that a *high threshold* corresponds to *low sensitivity*. The sensitivity measured in the light is called the light-adapted sensitivity, because it is measured while the eyes are adapted to the light. Because the room (or adapting) lights are on, the intensity of the flashing test light has to be high to be seen. At the beginning of the experiment, then, the threshold is high and the sensitivity is low.

Once the light-adapted sensitivity to the flashing test light is determined, the adapting light is extinguished so the participant is in the dark. The participant continues adjusting the intensity of the flashing light so he or she can just barely see it, tracking the increase in sensitivity that occurs in the dark. As the participant becomes more sensitive to the light, he or she must decrease the light's intensity to keep it just barely visible. The result, shown as the red curve in **Figure 3.13**, is a dark adaptation curve.

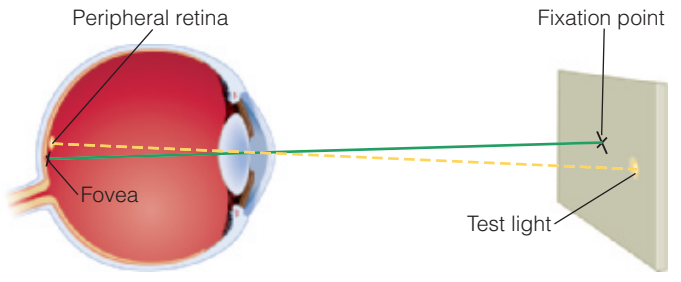

Figure 3.12 Viewing conditions for a dark adaptation experiment. In this example, the image of the fixation point falls on the fovea, and the image of the test light falls on the peripheral retina.

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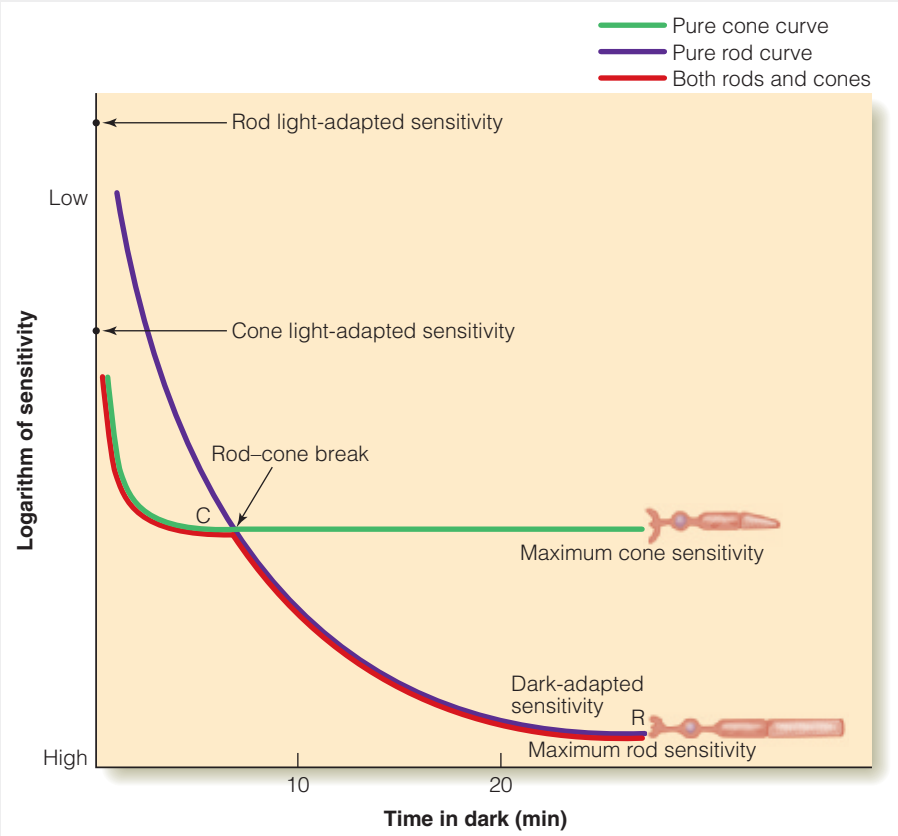

Figure 3.13 Three dark adaptation curves. The red line is the two-stage dark adaptation curve, with an initial cone branch and a later rod branch, which occurs when the test light is in the peripheral retina, as shown in Figure 3.12. The green line is the cone adaptation curve, which occurs when the test light falls on the fovea. The purple curve is the rod adaptation curve measured in a rod monochromat. Note that the downward movement of these curves represents an *increase* in sensitivity. The curves actually begin at the points indicating "light-adapted sensitivity," but there is a slight delay between the time the lights are turned off and when measurement of the curves begins.

The dark adaptation curve shows that as adaptation proceeds, the participant becomes more sensitive to the light. Note that higher sensitivity is at the bottom of this graph, so movement of the dark adaptation curve downward means that the participant's sensitivity is increasing. The red dark adaptation curve indicates that the participant's sensitivity increases in two phases. It increases rapidly for the first 3 to 4 minutes after the light is extinguished and then levels off. At about 7 to 10 minutes, it begins increasing again and continues to do so until the participant has been in the dark for about 20 or 30 minutes (Figure 3.13). The sensitivity at the end of dark adaptation, labeled **dark-adapted sensitivity**, is about 100,000 times greater than the light-adapted sensitivity measured before dark adaptation began.

Dark adaptation was involved in a 2007 episode of the *Mythbusters* program on the Discovery Channel, which was devoted to investigating myths about pirates. One of the myths was that pirates wore eye patches to preserve night vision in one eye so that when they went from the bright light outside to the darkness below decks, moving the patch to the light-adapted eye would enable them to see with the dark-adapted eye. To determine whether this would work, the Mythbusters carried out some tasks in a dark room just after both of their eyes had been in the light and did some different tasks with an eye that had previously been covered with a patch for 30 minutes. It isn't surprising that they completed the tasks much more rapidly when using the eye that had been patched. Anyone who has taken a course on sensation and perception could have told the Mythbusters that the eye patch would work because keeping an eye in the dark triggers the process of dark adaptation, which causes the eye to increase its sensitivity in the dark.

Whether pirates actually used patches to help them see below decks remains an unproven hypothesis. One argument against the idea that pirates wore eye patches to keep their sensitivity high is that patching one eye causes a decrease in depth perception, which might be a serious disadvantage when the pirate is working on deck. We will discuss why two eyes are important for depth perception in Chapter 10.

Although the Mythbusters showed that dark adapting one eye made it easier to see with that eye in the dark, we have a more specific goal. We are interested in showing that the first part of the dark adaptation curve is caused by the cones and the second part is caused by the rods. We will do this by running two additional dark adaptation experiments, one measuring adaptation of the cones and another measuring adaptation of the rods.

Measuring Cone Adaptation The reason the red curve in Figure 3.13 has two phases is that the flashing test light fell on the peripheral retina, which contains both rods and cones. To measure dark adaptation of the cones alone, we have to ensure that the image of the test light falls only on cones. We achieve this by having the participant look directly at the test light so its image falls on the all-cone fovea, and by making the test light small enough so that its entire image falls within the fovea. The dark adaptation curve determined by this procedure is indicated by the green line in Figure 3.13. This curve,

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which measures only the activity of the cones, matches the initial phase of our original dark adaptation curve but does not include the second phase. Does this mean that the second part of the curve is due to the rods? We can show that the answer to this question is "yes" by doing another experiment.

Measuring Rod Adaptation We know that the green curve in Figure 3.13 is due only to cone adaptation because our test light was focused on the all-cone fovea. Because the cones are more sensitive to light at the beginning of dark adaptation, they control our vision during the early stages of adaptation, so we can't determine what the rods are doing. In order to reveal how the sensitivity of the rods is changing at the very beginning of dark adaptation, we need to measure dark adaptation in a person who has no cones. Such people, who have no cones because of a rare genetic defect, are called **rod monochromats**. Their all-rod retinas provide a way for us to study rod dark adaptation without interference from the cones. (Students sometimes wonder why we can't simply present the test flash to the peripheral retina, which contains mostly rods. The answer is that there are enough cones in the periphery to influence the beginning of the dark adaptation curve.)

Because the rod monochromat has no cones, the light-adapted sensitivity we measure just before we turn off the lights is determined by the rods. The sensitivity we determine, which is labeled "rod light-adapted sensitivity" in Figure 3.13, indicates that the rods are much less sensitive than the cone light-adapted sensitivity we measured in our original experiment. We can also see that once dark adaptation begins, the rods increase their sensitivity, as indicated by the purple curve, and reach their final dark-adapted level in about 25 minutes (Rushton, 1961). The end of this rod adaptation measured in our monochromat matches the second part of the two-stage dark adaptation curve.

Based on the results of our dark adaptation experiments, we can summarize the process of dark adaptation. As soon as the light is extinguished, the sensitivity of *both* the cones *and* the rods begins increasing. However, because the cones are much more sensitive than the rods at the beginning of dark adaptation, we see with our cones right after the lights are turned out. One way to think about this is that the cones have "center stage" at the beginning of dark adaptation, while the rods are working "behind the scenes." However, after about 3 to 5 minutes in the dark, the cones have reached their maximum sensitivity, as indicated by the leveling off of the dark adaptation curve. Meanwhile, the rods are still adapting behind the scenes, and by about 7 minutes in the dark, the rods' sensitivity finally catches up to the cones'. The rods then become more sensitive than the cones, and rod adaptation, indicated by the second branch of the dark adaptation curve, becomes visible. The place where the rods begin to determine the dark adaptation curve instead of the cones is called the **rod–cone break**.

Why do the rods take about 20 to 30 minutes to reach their maximum sensitivity (point R on the curve) compared to only 3 to 4 minutes for the cones (point C)? The answer to this question involves a process called *visual pigment regeneration*, which occurs more rapidly in the cones than in the rods.

Visual Pigment Regeneration From our description of transduction earlier in the chapter, we know that light causes the retinal part of the visual pigment molecule, which is initially bent as shown in Figure 3.10a, to change its shape as in Figure 3.10b. This change from bent to straight is shown in the upper panels of Figure 3.14, which also shows how the retinal eventually separates from the *opsin* part of the molecule. This change in shape and separation from the opsin causes the molecule to become lighter in color, a process called **visual pigment bleaching**. This bleaching is shown in the lower panels of Figure 3.14. **Figure 3.14a** is a picture of a frog retina that was taken moments after it was illuminated with light.

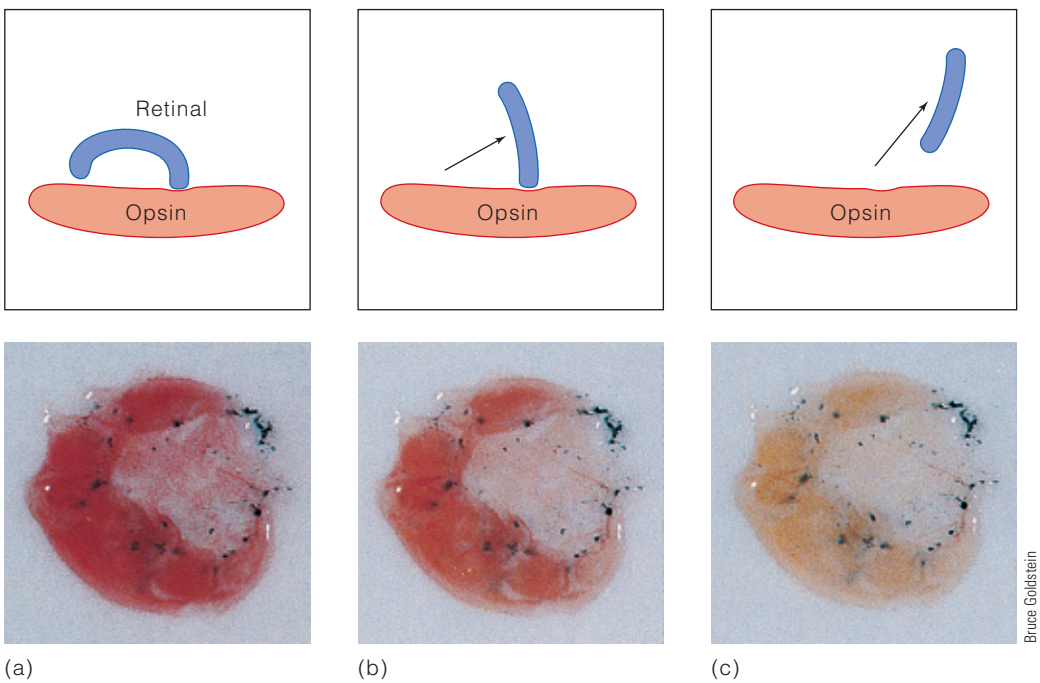

Figure 3.14 A frog retina was dissected from the eye in the dark and then exposed to light. The top row shows how the relationship between retinal and opsin changes after the retinal absorbs light. Only a small part of the opsin molecule is shown. The photographs in the bottom row show how the color of the retina changes after it is exposed to light. (a) This picture of the retina was taken just after the light was turned on. The dark red color is caused by the high concentration of visual pigment in the receptors that are still in the unbleached state. (b, c) After the retinal isomerizes, the retinal and opsin break apart, and the retina becomes bleached, as indicated by the lighter color.

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The red color is the visual pigment. As the light remains on, more and more of the pigment's retinal is isomerized and breaks away from the opsin, so the retina's color changes as shown in **Figures 3.14b** and **3.14c**.

When the pigments are in their lighter bleached state, they are no longer useful for vision. In order to do their job of changing light energy into electrical energy, the retinal needs to return to its bent shape and become reattached to the opsin. This process of reforming the visual pigment molecule is called **visual pigment regeneration**.

Another way to think about regeneration is to think about the visual pigment molecule as a light switch. Once you flip a light switch on by changing its position, you can't turn it on again until you turn it back off. Likewise, once a visual pigment molecule has signaled the presence of light by isomerizing (changing its position) and becoming bleached, as in Figure 3.14c, it can't signal the presence of light again until retinal reattaches to opsin, as in Figure 3.14a. Thus, the pigments become unresponsive to light in their bleached state and need time to regenerate before becoming responsive again.

When you are in the light, as you are now as you read this book, some of your visual pigment molecules are isomerizing and bleaching, as shown in Figure 3.14, while at the same time, others are regenerating. This means that in most normal light levels, your eye always contains some bleached visual pigment and some intact visual pigment. When you turn out the lights, the bleached visual pigment continues to regenerate, but there is no more isomerization, so eventually the concentration of regenerated pigment builds up so your retina contains only intact visual pigment molecules.

This increase in visual pigment concentration that occurs as the pigment regenerates in the dark is responsible for the increase in sensitivity we measure during dark adaptation. This relationship between pigment concentration and sensitivity was demonstrated by William Rushton (1961), who devised a procedure to measure the regeneration of visual pigment in humans by measuring the darkening of the retina that occurs during dark adaptation. (Think of this as Figure 3.14 proceeding from right to left.)

Rushton's measurements showed that cone pigment takes 6 minutes to regenerate completely, whereas rod pigment takes more than 30 minutes. When he compared the course of pigment regeneration to the dark adaptation curve, he found that the rate of cone dark adaptation matched the rate of cone pigment regeneration and the rate of rod dark adaptation matched the rate of rod pigment regeneration. These results demonstrated two important connections between perception and physiology:

1. Our sensitivity to light depends on the concentration of a chemical—the visual pigment.
2. The speed at which our sensitivity increases in the dark depends on a chemical reaction—the regeneration of the visual pigment.

What happens to vision if something prevents visual pigments from regenerating? This is what occurs when a person's retina becomes detached from the *pigment epithelium* (see Figure 3.2b), a layer that contains enzymes necessary for pigment regeneration. This condition, called **detached retina**, can occur as a result of traumatic injuries of the eye or head, as when a baseball player is hit in the eye by a line drive. When this occurs, the bleached pigment's separated retinal and opsin can no longer be recombined, and the person becomes blind in the area of the visual field served by the separated area of the retina. This condition is permanent unless the detached area of retina is reattached, which can be accomplished by laser surgery.

Spectral Sensitivity

Our discussion of rods and cones has emphasized how they control our vision as we adapt to darkness. Rods and cones also differ in the way they respond to light in different parts of the *visible spectrum* (Figure 1.23, page 18). The differences in the rod and cone responses to the spectrum have been studied by measuring the **spectral sensitivity** of rod vision and cone vision, where spectral sensitivity is the eye's sensitivity to light as a function of the light's wavelength. Spectral sensitivity is measured by determining the **spectral sensitivity curve**—the relationship between wavelength and sensitivity.

Spectral Sensitivity Curves The following is the psychophysical method used to measure a spectral sensitivity curve.

METHOD | Measuring a Spectral Sensitivity Curve

To measure sensitivity to light at each wavelength across the spectrum, we present one wavelength at a time and measure the participant's sensitivity to each wavelength. Light of a single wavelength, called monochromatic light, can be created by using special filters or a device called a *spectrometer*. To determine a person's spectral sensitivity, we determine the person's threshold for seeing monochromatic lights across the spectrum using one of the psychophysical methods for measuring threshold described in Chapter 1 (p. 14). The threshold is usually not measured at *every* wavelength, but at regular intervals. Thus, we might measure the threshold first at 400 nm, then at 410 nm, and so on. The result is the curve in **Figure 3.15a**, which shows that the threshold is higher at short and long wavelengths and lower in the middle of the spectrum; that is, less light is needed to see wavelengths in the middle of the spectrum than to see wavelengths at either the short- or long-wavelength end of the spectrum.

The ability to see wavelengths across the spectrum is often plotted not in terms of *threshold* versus wavelength, as in Figure 3.15a, but in terms of *sensitivity* versus wavelength. Using the equation, sensitivity = 1/threshold, we can convert the threshold curve in Figure 3.15a into the curve in **Figure 3.15b**, which is called the *spectral sensitivity curve*.

We measure the cone spectral sensitivity curve by having a participant look directly at a test light so that it stimulates only the cones in the fovea. We measure the rod spectral sensitivity curve by measuring sensitivity after the eye is dark adapted (so the rods control vision because they are the most sensitive photoreceptors) and presenting test flashes in the peripheral retina, off to the side of the fixation point.

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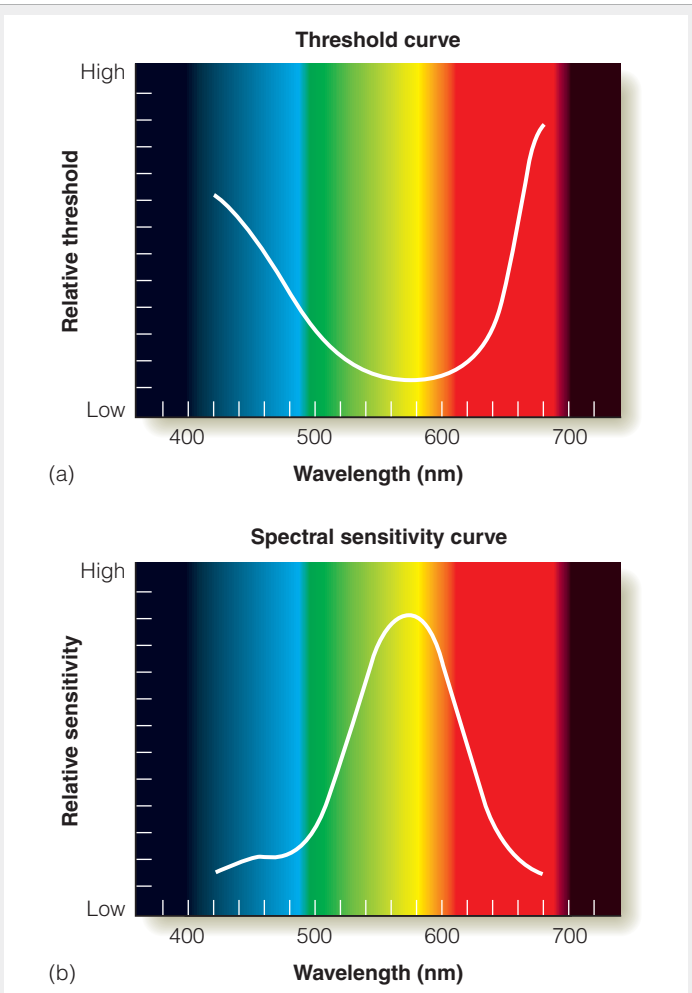

Figure 3.15 (a) The threshold for seeing a light as a function of wavelength. (b) Relative sensitivity as a function of wavelength—the *spectral sensitivity curve*. (Adapted from Wald, 1964)

The rod and cone spectral sensitivity curves in **Figure 3.16** show that the rods are more sensitive to short-wavelength light than are the cones, with the rods being most sensitive to light of 500 nm and the cones being most sensitive to light of 560 nm. This difference in the sensitivity of cones and rods to different wavelengths means that as vision shifts from the cones in the light-adapted eye to the rods after the eye has become dark adapted, our vision shifts to become relatively more sensitive to short-wavelength light—that is, light nearer the blue and green end of the spectrum.

You may have noticed an effect of this shift to short-wavelength sensitivity if you have observed how green foliage seems to stand out more near dusk. This enhanced perception of short wavelengths during dark adaptation is called the Purkinje (Pur-kin'-jee) shift after Johann Purkinje, who described this effect in 1825. You can experience this shift in color sensitivity during dark adaptation by closing one eye for 5 to 10 minutes so it dark adapts, then switching back and forth between your eyes and noticing how the blue flower in **Figure 3.17** is brighter compared to the red flower in your dark-adapted eye.

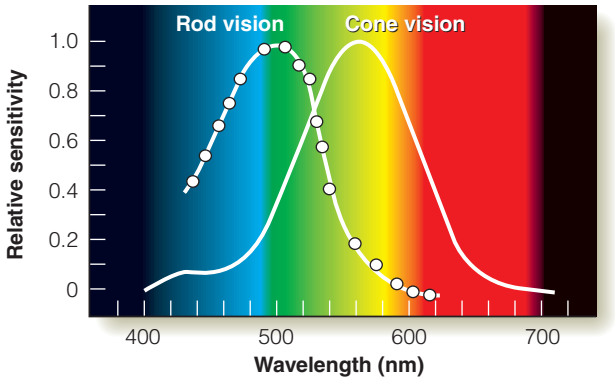

Figure 3.16 Spectral sensitivity curves for rod vision (left) and cone vision (right). The maximum sensitivities of these two curves have been set equal to 1.0. However, the relative sensitivities of the rods and the cones depend on the conditions of adaptation: The cones are more sensitive in the light, and the rods are more sensitive in the dark. The circles plotted on top of the rod curve are the absorption spectrum of the rod visual pigment. (From Wald & Brown, 1958)

Rod- and Cone-Pigment Absorption Spectra Just as we can trace the difference in the rate of rod and cone dark adaptation to a property of the visual pigments (the cone pigment regenerates faster than the rod pigment), we can trace the difference in the rod and cone spectral sensitivity curves to the rod and cone pigment *absorption spectra*. A pigment's absorption spectrum is a plot of the amount of light absorbed versus the wavelength of the light. The absorption spectra of the rod and cone pigments are shown in **Figure 3.18**. The rod pigment absorbs best at 500 nm, the blue-green area of the spectrum.

There are three absorption spectra for the cones because there are three different cone pigments, each contained in its own receptor. The short-wavelength pigment (S) absorbs light best at about 419 nm; the medium-wavelength pigment (M) absorbs light best at about 531 nm; and the long-wavelength pigment (L) absorbs light best at about 558 nm. We will have more to say about the three cone pigments in Chapter 9, because they are the basis of our ability to see colors.

The absorption of the rod visual pigment closely matches the rod spectral sensitivity curve (Figure 3.18), and the short-, medium-, and long-wavelength cone pigments add together to result in a psychophysical spectral sensitivity curve that

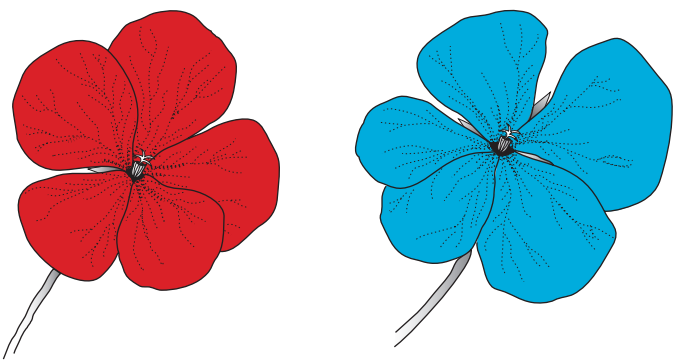

Figure 3.17 Flowers for demonstrating the Purkinje shift. See text for explanation.

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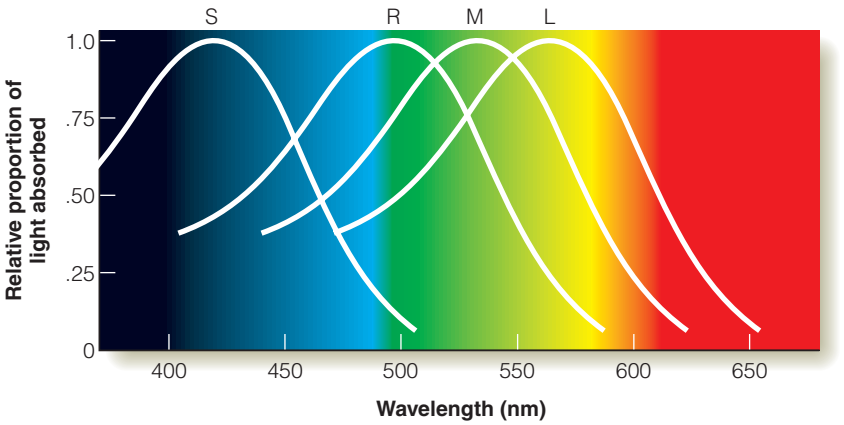

Figure 3.18 Absorption spectra of the rod pigment (R), and the short- (S), medium- (M), and long-wavelength (L) cone pigments. (Based on Dartnall, Bowmaker, & Mollon, 1983)

peaks at 560 nm. Because there are fewer short-wavelength receptors and therefore much less of the short-wavelength pigment, the cone spectral sensitivity curve is determined mainly by the medium- and long-wavelength pigments (Bowmaker & Dartnall, 1980; Stiles, 1953).

It is clear from the evidence we have presented that the increase in sensitivity that occurs in the dark (dark adaptation) and the sensitivity to different wavelengths across the spectrum (spectral sensitivity) are determined by the properties of the rod and cone visual pigments. Thus, even though perception—the experience that results from stimulation of the senses—does not occur in the eye, our experience is definitely affected by what happens there.

We have now traveled through the first three steps in the perceptual process for the sense of vision. The tree (Step 1) reflects light, which is focused onto the retina by the eye's optical system (Step 2). The photoreceptors shape perception as they transform light energy into electrical energy (Step 3). We are now ready to discuss the processing that occurs after the photoreceptors as the signal moves through the other cells in the retina (Step 4).

TEST YOURSELF 3.1

1. Describe light, the structure of the eye, and the rod and cone receptors. How are the rods and cones distributed across the retina?
2. How does moving an object closer to the eye affect how light reflected from the object is focused on the retina?
3. How does the eye adjust the focusing of light by accommodation? Describe the following refractive errors that can cause problems in focusing: presbyopia, myopia, hyperopia. How are these problems solved through either accommodation or corrective lenses?
4. Where on the retina does a researcher need to present a stimulus to test dark adaptation of the cones? How is this related to the distribution of the rods and cones on the retina? How can the adaptation of cones be measured without any interference from the rods? How can adaptation of the rods be measured without any interference from the cones?
5. Describe how rod and cone sensitivity changes starting when the lights are turned off and how this change in sensitivity continues for 20 to 30 minutes in the dark. When do the rods begin adapting? When do the rods become more sensitive than the cones?
6. What happens to visual pigment molecules when they (a) absorb light and (b) regenerate? What is the connection between visual pigment regeneration and dark adaptation?
7. What is spectral sensitivity? How is a cone spectral sensitivity curve determined? A rod spectral sensitivity curve?
8. What is a pigment absorption spectrum? How do rod and cone pigment absorption spectra compare, and what is their relationship to rod and cone spectral sensitivity?

3.4 What Happens as Signals Travel Through the Retina

We have now seen how the photoreceptors are critical to perception since they transduce incoming light into an electrical signal. They also influence perception in the different ways that rods versus cones adapt to the dark and respond to different wavelengths of light. As we will discuss in this section, the way in which the photoreceptors and the other cells in the retina are "wired up" also has a substantial effect on our perception.

Rod and Cone Convergence

Figure 3.19a is a cross section of a monkey retina that has been stained to reveal the retina's layered structure. **Figure 3.19b** shows the five types of neurons that make up these layers and that create **neural circuits**—interconnected groups of neurons—within the retina. Signals generated in the receptors (R) travel to the **bipolar cells** (B) and then to the **ganglion cells** (G). The receptors and bipolar cells do not have long axons, but the ganglion cells do. These long axons transmit signals out of the retina in the optic nerve (see Figure 3.6).

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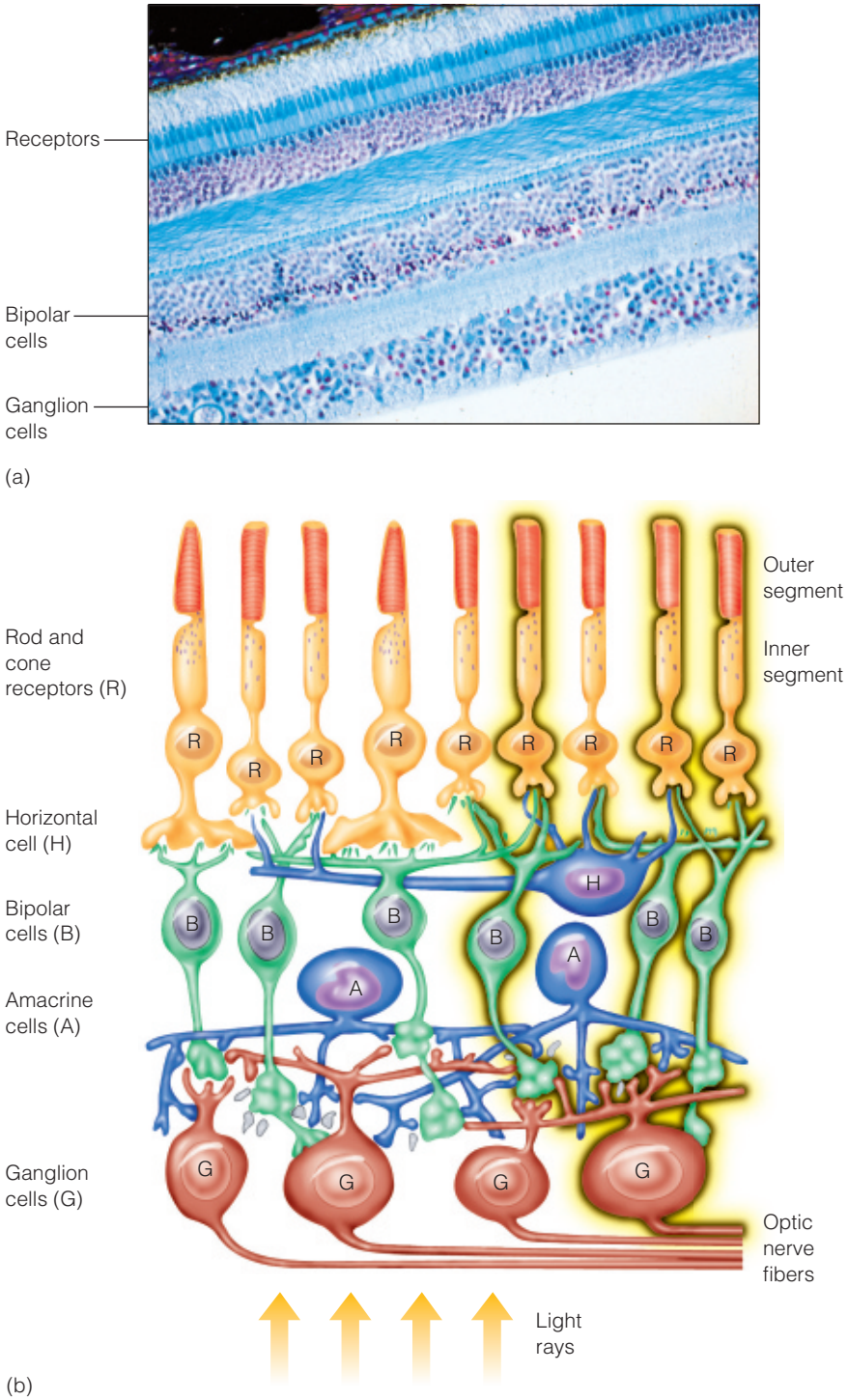

Figure 3.19 (a) Cross section of a monkey retina, which has been stained to show the various layers. Light is coming from the bottom. The purple circles are cell bodies of the receptors, bipolar cells, and ganglion cells. (b) Cross section of the primate retina showing the five major cell types and their interconnections: receptors (R), bipolar cells (B), ganglion cells (G), horizontal cells (H), and amacrine cells (A). Signals from the three highlighted rods on the right reach the highlighted ganglion cell. This is an example of convergence. (Based on Dowling & Boycott, 1966)

In addition to the photoreceptors, bipolar cells, and ganglion cells, there are two other types of neurons that connect neurons across the retina: **horizontal cells** and **amacrine cells**. Signals can travel between receptors through the horizontal cells, and between bipolar cells and between ganglion cells through the amacrine cells. We will return to the horizontal and amacrine cells later in this chapter. For now we will focus on the direct pathway from the photoreceptors to the ganglion cells. We focus specifically on the property of *neural convergence*.

Perception Is Shaped by Neural Convergence

Neural convergence (or just **convergence** for short) occurs when a number of neurons synapse onto a single neuron. A great deal of convergence occurs in the retina because each eye has 126 million photoreceptors but only 1 million ganglion cells. Thus, on the average, each ganglion cell receives signals from 126 photoreceptors. We can show how convergence can affect perception by returning to the rods and cones. An important difference between rods and cones is that the signals from

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the rods converge more than do the signals from the cones. We can appreciate this difference by noting that there are 120 million rods in the retina, but only 6 million cones. Thus, on the average, about 120 rods send their signals to one ganglion cell, but only about 6 cones send signals to a single ganglion cell.

This difference between rod and cone convergence becomes even greater when we consider the cones in the fovea. (Remember that the fovea is the small area that contains only cones.) Many of these foveal cones have "private lines" to ganglion cells, so that each ganglion cell receives signals from only one cone, with no convergence. The greater convergence of the rods compared to the cones translates into two differences in perception: (1) the rods result in better sensitivity than the cones, and (2) the cones result in better detail vision than the rods.

Convergence Causes the Rods to Be More Sensitive Than the Cones In the dark-adapted eye, rod vision is more sensitive than cone vision (see "dark-adapted sensitivity" in the dark adaptation curve of Figure 3.13). This is why in dim light we use our rods to detect faint stimuli. A demonstration of this effect, which has long been known to astronomers and amateur stargazers, is that some very dim stars are difficult to detect when looked at directly (because the star's image falls on the cones in the fovea), but these same stars can often be seen when they are located off to the side of where the person is looking (because then the star's image falls on the rod-rich peripheral retina). One reason for this greater sensitivity of rods, compared to cones, is that it takes less light to generate a response from an individual rod receptor than from an individual cone receptor (Barlow & Mollon, 1982; Baylor, 1992). But there is another reason as well: The rods have greater convergence than the cones.

Keeping this basic principle in mind, we can see how the difference in rod and cone convergence translates into differences in the maximum sensitivities of the rods and the cones by considering the two circuits in **Figure 3.20**. The left panel shows five rod receptors converging onto one ganglion cell, and the right panel shows five cone receptors each sending signals onto their own ganglion cells. This represents the greater convergence of the rods than the cones. Note that we have left out the bipolar, horizontal, and amacrine cells in these circuits for simplicity, but our conclusions are not affected by these omissions.

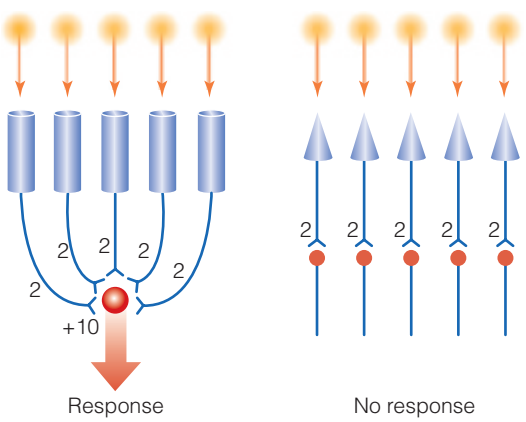

Figure 3.20 The wiring of the rods (left) and the cones (right). The yellow dot and arrow above each receptor represents a "spot" of light that stimulates the receptor. The numbers represent the number of response units generated by the rods and the cones in response to a spot intensity of 2.

For the purposes of our discussion, we will assume that we can present small spots of light to individual rods and cones. Let's also say that when a photoreceptor is stimulated by one spot of light, it causes one *unit of excitation* in the ganglion cell, and it takes 10 *units of excitation* for the ganglion cell to fire. Each ganglion cell can sum all of the inputs from the photoreceptors to try to reach this 10-unit threshold.

If we present spots of light with an intensity of 1 to each photoreceptor, the rod ganglion cell receives 5 units of excitation, 1 from each of the 5 rod receptors. In contrast, each cone ganglion cell receives just 1 unit of excitation, 1 from each cone receptor. Thus, when intensity = 1, the rod ganglion cell receives more excitation than the cone ganglion cells because of convergence, but not enough to cause it to fire.

If, however, we increase the intensity to 2, as shown in Figure 3.20, the rod ganglion cell receives 2 units of excitation from each of its 5 receptors, for a total of 10 units of excitation. This causes the ganglion cell to fire, and the light is perceived. Meanwhile, at the same intensity, the cones' ganglion cells are each receiving only 2 units of excitation, so those ganglion cells have no response, since the 10-unit threshold has not been reached. For the cones' ganglion cells to fire, we would have to increase the intensity of the light.

This example shows that it takes less incoming light to stimulate a ganglion cell that is receiving input from rods, since many rods converge onto that one ganglion cell. On the contrary, it takes much more light to stimulate a ganglion cell that receives input from cones, since fewer cones converge onto each ganglion cell. This demonstrates how the rods' high sensitivity compared to the cones' is caused by the rods' greater convergence.

The fact that rod and cone sensitivity is determined not by individual receptors but by groups of receptors converging onto other neurons means that when we describe "rod vision" and "cone vision" we are actually referring to the way *groups* of rods and cones participate in determining our perceptions.

Less Convergence Causes the Cones to Have Better Acuity Than the Rods While rod vision is more sensitive than cone vision because the rods have *more* convergence, the cones have better visual acuity because they have *less* convergence. Acuity refers to the ability to see details; thus, being able to see very small letters on an eye chart in the optometrist's or ophthalmologist's office translates into high acuity. (Also, remember grating acuity from Chapter 1, page 12.)

One way to appreciate the high acuity of the cones is to think about the last time you were looking for one thing that was hidden among many other things. This could be searching for your cellphone on the clutter of your desk or locating a friend's face in a crowd. To find what you are looking for, you usually need to move your eyes from one place to another. When you move your eyes to look at different things in this way, what you are doing is scanning with your cone-rich fovea (remember that when you

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look directly at something, its image falls on the fovea). This is necessary because your visual acuity is highest in the fovea; objects that are imaged on the peripheral retina are not seen as clearly.

DEMONSTRATION | Foveal Versus Peripheral Acuity

D I H C N R L A Z I F W N S M Q Z K D X

You can demonstrate that foveal vision is superior to peripheral vision for seeing details by looking at the X on the right and, without moving your eyes, seeing how many letters you can identify to the left. If you do this without cheating (resist the urge to look to the left!), you will find that although you can read the letters right next to the X, which are imaged on or near the fovea, it is difficult to read letters that are further off to the side, which are imaged on the peripheral retina.

This demonstration shows that acuity is better in the fovea than in the periphery. Because you were light adapted, the comparison in this demonstration was between the foveal cones, which are tightly packed, and the peripheral cones, which are more widely spaced. Comparing the foveal cones to the rods results in even greater differences in acuity. We can make this comparison by noting how acuity changes during dark adaptation.

The picture of the bookcase in **Figure 3.21** simulates the change in acuity that occurs during dark adaptation. The books on the top shelf represent the details seen when viewing the books in the light, when cones are controlling vision. The middle shelf represents detail perception midway through dark adaptation, when the rods are beginning to determine vision, and the books on the bottom shelf represent the poor detail vision of the rods. Also note that color has disappeared, because color vision depends on the cones, as we will see in Chapter 9. The chapter-opening picture on page 38 also illustrates what happens when vision shifts from cones to rods.

Bruce Goldstein

Figure 3.21 Simulation of the change from colorful sharp perception to colorless fuzzy perception that occurs during the shift from cone vision to rod vision during dark adaptation. The top shelf simulates cone vision; the bottom shelf, rod vision.

We can understand how differences in rod and cone wiring explain the cones' greater acuity by returning to our rod and cone neural circuits. First consider the rod circuit in **Figure 3.22a**. When we present two spots of light next to each other, as on the left, the rods' signals cause the ganglion cell to fire. When we separate the two spots, as on the right, the two separated rods still feed into the same ganglion cell and cause it to fire. In both cases, the ganglion cell fires. Thus, firing of the ganglion cell provides no information about whether there are two spots close together or two separated spots.

We now consider the cones in **Figure 3.22b**, each of which synapses on its own ganglion cell. When we present a light that

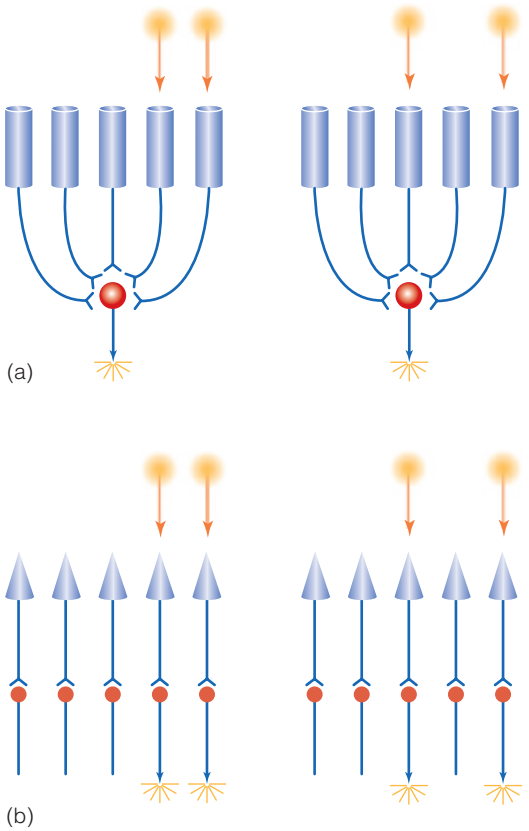

Figure 3.22 How the wiring of the rods and cones determines detail vision. (a) Rod neural circuits. On the left, stimulating two neighboring rods causes the ganglion cell to fire. On the right, stimulating two separated rods causes the same effect. (b) Cone neural circuits. On the left, stimulating two neighboring cones causes two neighboring ganglion cells to fire. On the right, stimulating two separated cones causes two separated ganglion cells to fire. This firing of two neurons, with a space between them, indicates that two spots of light have been presented to the cones.

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stimulates two neighboring cones, as on the left, two adjacent ganglion cells fire. But when we separate the spots, as on the right, two separate ganglion cells fire. This separation between two firing cells provides information that there are two separate spots of light. Thus, the cones' lack of convergence causes cone vision to have higher acuity than rod vision.

Convergence is therefore a double-edged sword. High convergence results in high sensitivity but poor acuity (the rods). Low convergence results in low sensitivity but high acuity (cones). The way the rods and cones are wired up in the retina, therefore, influences what we perceive. We now continue our description of processing in the retina, by looking at a property discovered in retinal ganglion cells called the *receptive field*.

Ganglion Cell Receptive Fields

Signals from the photoreceptors travel through the retina and eventually reach the retinal ganglion cells (Figure 3.19). The axons of the ganglion cells leave the retina as fibers of the optic nerve (**Figure 3.23**). Pioneering research by H. Keffer Hartline (1938, 1940), which won him the Nobel Prize in Physiology and Medicine in 1967, led to the discovery of a property of neurons called the neuron's *receptive field*.

Hartline's Discovery of Receptive Fields In his seminal research, Hartline isolated a single ganglion cell axon in the opened eyecup of a frog (Figure 3.24) by teasing apart the optic nerve near where it leaves the eye. While recording from this axon, Hartline illuminated different areas of the retina and found that the cell he was recording from responded only when a small area of the retina was illuminated. He called the area that caused the neuron to fire the ganglion cell's receptive field (**Figure 3.24a**), which he defined as "the region of the retina that must receive illumination in order to obtain a response in any given fiber" (Hartline, 1938, p. 410).

Hartline went on to emphasize that a ganglion cell's receptive field covers a much greater area than a single photoreceptor.

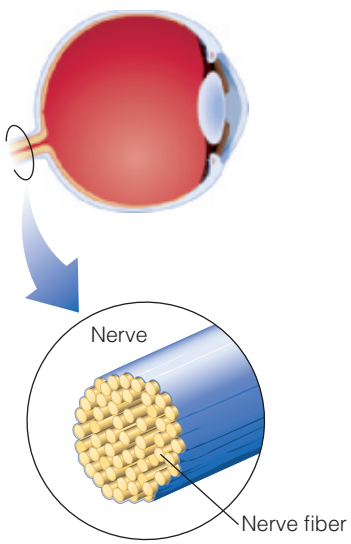

Figure 3.23 The optic nerve, which leaves the back of the eye, contains about one million ganglion cell axons, or nerve fibers.

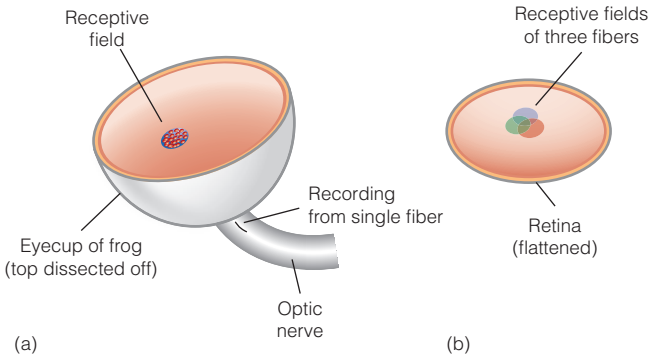

Figure 3.24 (a) Hartline's experiment in which he presented stimuli to the retina by dissecting a frog's eye and removing the top to create an "eyecup." He then presented light to the retina to determine which area of a frog's retina caused firing in one of the ganglion cell fibers in the optic nerve. This area is called the *receptive field* of that ganglion cell. (b) Receptive fields of three ganglion cells. These receptive fields overlap, so stimulating at a particular point on the retina will generally activate a number of fibers in the optic nerve.

The fact that a ganglion cell's receptive field covers hundreds or even thousands of receptors means that the cell is receiving converging signals from all of these photoreceptors, as we saw in the previous section. Finally, Hartline noted that the receptive fields of many different ganglion cells overlap (**Figure 3.24b**). This means that shining light on a particular point on the retina activates many ganglion cells.

One way to think about receptive fields is to imagine a football field and a grandstand full of spectators, each with a pair of binoculars trained on one small area of the field. Each spectator is monitoring what is happening in his or her own small area, and all of the spectators together are monitoring the entire field. Since there are so many spectators, some of the areas they are observing will wholly or partially overlap.

To relate this football field analogy to Hartline's receptive fields, we can equate each spectator to a ganglion cell, the football field to the retina, and the small areas viewed by each spectator to receptive fields. Just as each spectator monitors a small area of the football field, but collectively all spectators take in information about what is happening on the entire football field, each ganglion cell monitors a small area of retina. However, because there are many ganglion cells, just as there are many spectators, all of them together take in information about what is happening over the entire retina.

Kuffler's Discovery of Center-Surround Receptive Fields Following Hartline's research on the receptive fields of ganglion cells in the frog's retina, Stephen Kuffler (1953) measured ganglion cell receptive fields in the cat and reported a property of these receptive fields that Hartline had not observed in the frog. In the cat (and, as it turns out, in other mammals such as monkeys and humans), the ganglion cells have center-surround receptive fields that are arranged like concentric circles in a center-surround organization, as shown in Figure 3.25. In the these receptive fields, the area in the

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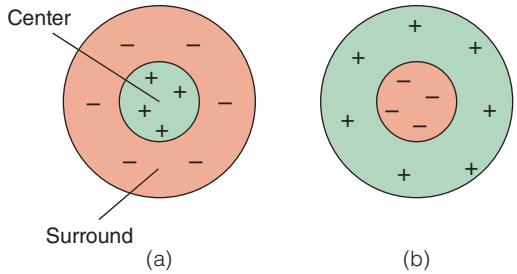

Figure 3.25 Center-surround receptive fields: (a) excitatory center, inhibitory surround; (b) inhibitory center, excitatory surround.

"center" of the receptive field responds differently to light than the area in the "surround" of the receptive field (Barlow et al., 1957; Hubel & Wiesel, 1965; Kuffler, 1953).

For example, for the receptive field in **Figure 3.25a**, presenting a spot of light to the center increases firing, so it is called the **excitatory area** of the receptive field. In contrast, stimulation of the surround causes a decrease in firing, so it is called the **inhibitory area** of the receptive field. This receptive field is called an **excitatory-center, inhibitory-surround receptive field**. The receptive field in **Figure 3.25b**, which responds with inhibition when the center is stimulated and excitation when the surround is stimulated, is an **inhibitory-center, excitatory-surround receptive field**. Both of these types of center-surround ganglion cell receptive fields are present in the mammalian retina.

The discovery that receptive fields can have oppositely responding areas made it necessary to modify Hartline's definition of receptive field to "the retinal region over which a cell in the visual system can be influenced (excited or inhibited) by light" (Hubel & Wiesel, 1961). The word *influenced* and reference to excitation and inhibition make it clear that *any* change in firing—either an increase or a decrease—needs to be taken into account in determining a neuron's receptive field.

The discovery of center-surround receptive fields was also important because it showed that ganglion cells respond best to specific patterns of illumination. This is illustrated by an effect called **center-surround antagonism**, illustrated in **Figure 3.26**. A small spot of light presented to the excitatory center of the receptive field causes a small increase in the rate of nerve firing (a); increasing the light's size so that it covers the entire center of the receptive field increases the cell's response, as shown in (b).

Center-surround antagonism comes into play when the spot of light becomes large enough that it begins to cover the inhibitory area, as in (c) and (d). Stimulation of the inhibitory surround counteracts the center's excitatory response, causing a decrease in the neuron's firing rate. Thus, because of center-surround antagonism, this neuron responds best to a spot of light that is the size of the excitatory center of the receptive field.

How does center-surround antagonism work? To answer this question, we need to return to our discussion of neural convergence and consider how inhibition and convergence work together. Specifically, the inhibition involved in center-surround ganglion cell receptive fields is known as **lateral inhibition**—inhibition that is transmitted *across* the retina (laterally).

Lateral Inhibition Underlies Center-Surround Antagonism The pioneering work on lateral inhibition was carried out by Keffer Hartline, Henry Wagner, and Floyd Ratliff (1956) on a primitive animal called the *Limulus*, more familiarly known as the horseshoe crab (**Figure 3.27**). They chose the *Limulus* because the structure of its eye makes it possible to stimulate individual receptors. The *Limulus* eye is made up of hundreds of tiny structures called **ommatidia**, and each ommatidium has a small lens on the eye's surface that is located directly over a single receptor. Each lens and receptor is roughly the diameter of a pencil point (very large compared to human receptors), so it is possible to illuminate and record from a single receptor without illuminating its neighboring receptors.

When Hartline and coworkers recorded from the nerve fiber of receptor A, as shown in **Figure 3.28**, they found that illumination of that receptor caused a large response (**Figure 3.28a**). But when they added illumination to the three nearby receptors at B, the response of receptor A decreased (**Figure 3.28b**). They also found that further increasing the illumination of B decreased A's response even more (**Figure 3.28c**). Thus, illumination of the neighboring

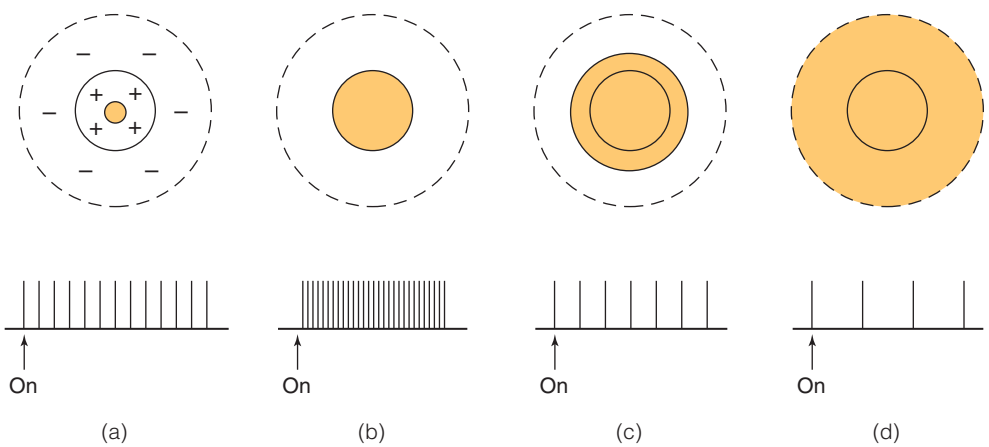

Figure 3.26 Response of an excitatory-center, inhibitory-surround ganglion cell receptive field as stimulus size is increased. Color indicates the area stimulated with light. The response to the stimulus is indicated below each receptive field. (a) Small response to a small dot in the excitatory center. (b) Increased response when the whole excitatory area is stimulated. (c) Response begins to decrease when the size of the spot is increased so that it stimulates part of the inhibitory surround; this illustrates center-surround antagonism. (d) Covering all of the inhibitory surround decreases the response further.

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Bruce Goldstein

Figure 3.27 A *Limulus*, or horseshoe crab. Its large eyes are made up of hundreds of ommatidia, each containing a single receptor.

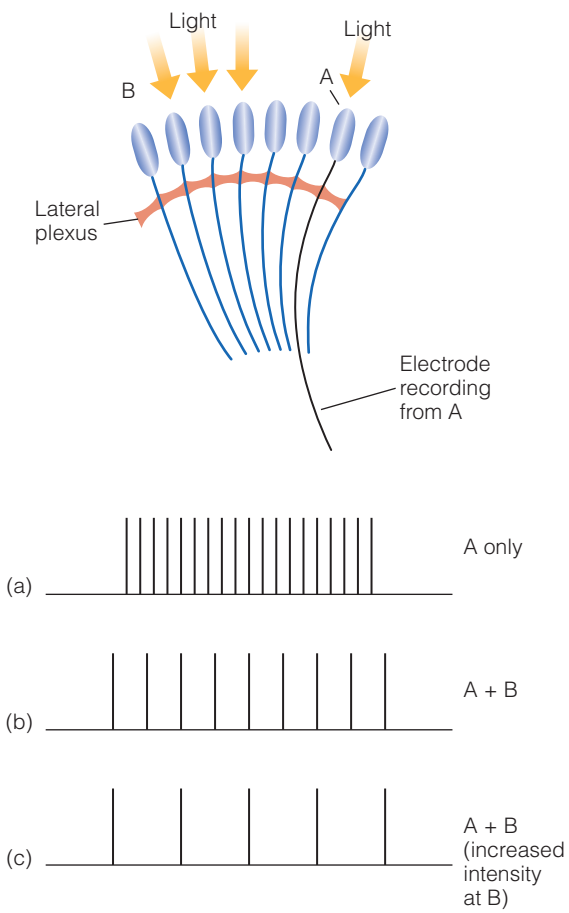

Figure 3.28 A demonstration of lateral inhibition in the *Limulus*. The records show the response recorded by the electrode in the nerve fiber of receptor A: (a) when only receptor A is stimulated; (b) when receptor A and the receptors at B are stimulated together; (c) when A and B are stimulated, with B stimulated at an increased intensity. (Adapted from Ratliff, 1965)

receptors at B inhibited the firing caused by stimulation of receptor A. This decrease in the firing of receptor A is caused by lateral inhibition that is transmitted from B to A across the *Limulus*'s eye by the fibers of the *lateral plexus*, shown in Figure 3.28.

Just as the lateral plexus transmits signals laterally in the *Limulus*, the horizontal and amacrine cells (see Figure 3.19, page 52) transmit inhibitory signals laterally across the monkey and human retina. This lateral inhibition by the horizontal and amacrine cells is what underlies center-surround antagonism in center-surround ganglion cell receptive fields.

To help us understand the relationship between center-surround receptive fields, convergence, and lateral inhibition, let's consider an example of a neural circuit in the retina that demonstrates all of these principles working together. **Figure 3.29** shows a neural circuit consisting of seven photoreceptors. These neurons, with the aid of lateral inhibition, help create the excitatory-center, inhibitory-surround receptive field of neuron B.

Receptors 1 and 2 converge on neuron A; receptors 3, 4, and 5 converge on neuron B; and receptors 6 and 7 converge on neuron C. All of these synapses are excitatory, as indicated by the blue Y-shaped connections and + signs. Additionally, neurons A and C (representing horizontal/amacrine cells) are laterally connected to neuron B, with both of these synapses being inhibitory, as indicated by the red T-shaped connections and − signs. Let's now consider how stimulating the photoreceptors will affect the firing of B. Stimulating receptors 3, 4, and 5 causes B's firing to increase because their synapses with B are excitatory. This is what we would expect, because receptors 3, 4, and 5 are located in the excitatory center of the receptive field.

Now consider what happens when we stimulate receptors 1 and 2, located in the surround of the receptive field. These receptors connect to neuron A with excitatory synapses, so illuminating these receptors causes A's firing to increase. A's signal then travels to neuron B, but because its synapse onto B is inhibitory, this signal causes B's firing to decrease. This is what we would expect, because receptors 1 and 2 are located in the inhibitory surround of the receptive field. The same thing happens when we illuminate receptors 6 and 7, which are also located in the inhibitory surround. Thus, stimulating anywhere in the center (green area) causes B's firing to increase. Stimulating anywhere in the surround (red area) causes B's firing to decrease due to lateral inhibition.

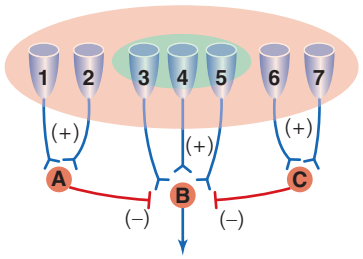

Figure 3.29 A seven-receptor neural circuit underlying a center-surround receptive field. Receptors 3, 4, and 5 are in the excitatory center, and receptors 1, 2, 6, and 7 are in the inhibitory surround.

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Neuron B sums all of its incoming signals to produce one response—a general principle of neurons introduced in Chapter 2. So, when the entire receptive field is illuminated, neuron B receives *both* an excitatory signal from the center *and* inhibitory signals from the surround through lateral inhibition. Those inputs would counteract each other, causing center-surround antagonism. Although an actual ganglion cell neuron receives signals from many more than seven photoreceptors, and the wiring diagram is much more complex than shown in our example, the basic principle described here operates: Center-surround receptive fields are created by the interplay of excitation and lateral inhibition.

Center-Surround Receptive Fields and Edge Enhancement Center-surround receptive fields illustrate how the interaction between excitatory and inhibitory connections can shape the responding of individual neurons, as when ganglion cells respond best to small spots of light (Figure 3.26). But in addition to determining optimal stimuli for ganglion cells, center-surround receptive fields contribute to edge enhancement—an increase in perceived contrast at borders between regions of the visual field. In other words, they help to make edges look more distinct so that we can see them more easily.

To illustrate edge enhancement, let's look at **Figure 3.30a**, which shows two side-by-side rectangles. An important feature of these rectangles is revealed by plotting the light intensity that would be measured by a light meter scanning the rectangles along the line from A to D (**Figure 3.30b**). Notice that the light intensity remains the same across the entire distance between A and B, then at the border the intensity drops to a lower level and remains the same between C and D.

However, you may notice that although the *intensity* is the same from A to B, and then from C to D, the *perception of lightness* is not. At the border between B and C there is a lightening at B to the left of the border and a darkening at C to the right of the border. The perceived light and dark bands at the borders, which are not present in the actual physical stimuli, is called the Chevreul illusion named after the French chemist Michel-Eugene Chevreul (1789–1889) who, as the director of dyes at the Gobelin tapestry works, became interested in how placing colors side by side could alter their appearance. The perceived light and dark bands are represented in **Figure 3.30c**, which shows the light band at B as an upward bump in lightness, and the dark band at C as a downward bump in lightness. By appearing lighter on one side of the border and darker on the other, the edge itself looks sharper and more distinct, which demonstrates edge enhancement.

Illusory light and dark bars at borders also occur in the environment, especially in shadows. You might notice this if there are shadows nearby, or see if you can find light and dark bars in **Figure 3.31**. This figure shows a fuzzy shadow border between light and dark, rather than the sharp border in the Chevreul display. Light and dark bands created at fuzzy borders are called Mach bands, after German physicist Ernst Mach (1836–1916). The same mechanism is thought to be responsible for the Mach and Chevreul effects.

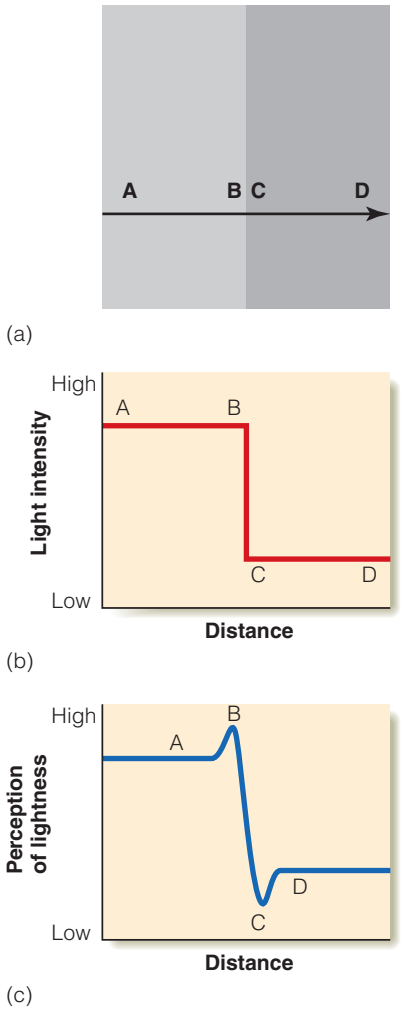

Figure 3.30 The Chevreul illusion. Look at the borders between light and dark. (a) Just to the left of the border, near B, a faint light band can be perceived, and just to the right at C, a faint dark band can be perceived. (b) The physical intensity distribution of the light, as measured with a light meter. Because the intensity plot looks like a step in a staircase, this illusion is also called the staircase illusion. (c) A plot showing the perceptual effect described in (a). The bump in the curve at B indicates the light band, and the dip in the curve at C indicates the dark band. The bumps that represent our perception of the bands are not present in the physical intensity distribution.

We can understand how center-surround receptive fields can explain the edge enhancement in the Chevreul and Mach illusions by looking at **Figure 3.32**, which shows the locations of the excitatory-center inhibitory-surround receptive fields (RFs) of four ganglion cells. The key to understanding how these neurons could cause edge enhancement is to compare the amount of inhibition for the different cells. Let's consider A and B first. The inhibitory area of A's receptive field is all in the lighter region (indicated by the dots), so generates a lot of inhibition, which decreases the cell's firing rate. But only part of the inhibitory area of cell B's receptive field is in the lighter region, so the cell B's response is greater than cell A's response, thereby creating the light band at B.

Now let's consider C and D. Cell C generates more inhibition, because part of its inhibitory surround is in the lighter

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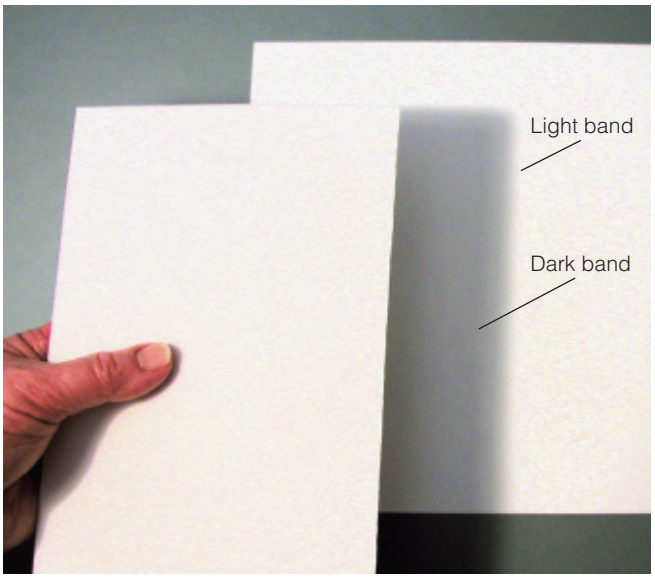

Figure 3.31 Shadow-casting technique for observing illusory bands in shadows. Illuminate a light-colored surface with a lamp and cast a shadow with a piece of paper. When the transition from light to dark is gradual, rather than a step as in the Chevreul illusion, the bands are called *Mach bands*.

region, whereas none of D's inhibitory surround is in the lighter region. Thus, cell C's response is less than cell D's response, which creates the dark band at C.

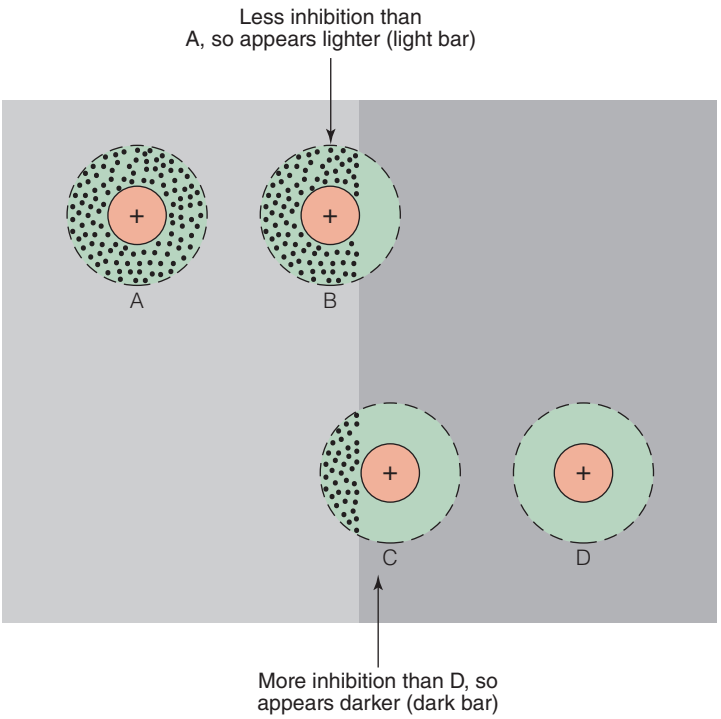

Figure 3.32 How the Chevreul illusions can be explained by center-surround receptive fields and lateral inhibition. Areas of the inhibitory surround of the receptive field that are illuminated by the more intense light on the light side of the border are indicated by dots. Greater areas of high illumination result in more inhibition, which decreases neural responding.

Of course, the actual situation is more complicated than this because hundreds or thousands of ganglion cells could be firing to the two rectangles. But our example illustrates how neural processing involving excitation and inhibition can create perceptual effects—in this case, enhanced borders.

The important message for our purposes is that perception is the outcome of neural processing—in this example, the neural processing that occurs in center-surround receptive fields in the retina. As we will see in the next chapter when we consider the brain, receptive fields change as we move to higher levels of the visual system so that the higher-level neurons respond to more complex stimuli (like objects instead of just edges), which makes it easier to draw relationships between neural processing and perception.

SOMETHING TO CONSIDER:

Early Events Are Powerful

In 1990, a rocket blasted off from Cape Canaveral to place the Hubble space telescope into earth orbit. The telescope's mission was to provide high-resolution images from its vantage point above the interference of the earth's atmosphere. But it took only a few days of data collection to realize that something was wrong. Images of stars and galaxies that should have been extremely sharp were blurred (**Figure 3.33a**). The cause of the problem, it turned out, was that the telescope's lens was ground to the wrong curvature. Although a few of the planned observations were possible, the telescope's mission was severely compromised. Three years later, the problem was solved when a corrective lens was fitted over the original one. The new Hubble, with its "eyeglasses," could now see stars as sharp points (**Figure 3.33b**).

This diversion to outer space emphasizes that what happens early in a system can have a large, often crucial, effect on the outcome. No matter how sophisticated Hubble's electronic computer and processing programs were, the distorted image caused by the faulty lens had fatal effects on the quality of the telescope's image. Similarly, if problems in the eye's focusing system deliver degraded images to the retina, no amount of processing by the brain can create sharp perception.

What we see is also determined by the energy that can enter the eye and can activate the photoreceptors. Although there is a huge range of electromagnetic energy in the environment, the visual pigments in the receptors limit our sensitivity by absorbing only a narrow range of wavelengths, as we introduced in this chapter. One way to think about the effect of pigments is that they act like filters, only making available for vision the wavelengths they absorb. Thus, at night, when we are perceiving with our rods, we see only wavelengths between about 420 and 580 nm, with the best sensitivity at 500 nm. However, in daylight, when we are perceiving with our cones, we become more sensitive to longer wavelengths, as the best sensitivity shifts to 560 nm.

This idea of visual pigments as limiting our range of seeing is dramatically illustrated by the honeybee, which, as we will see

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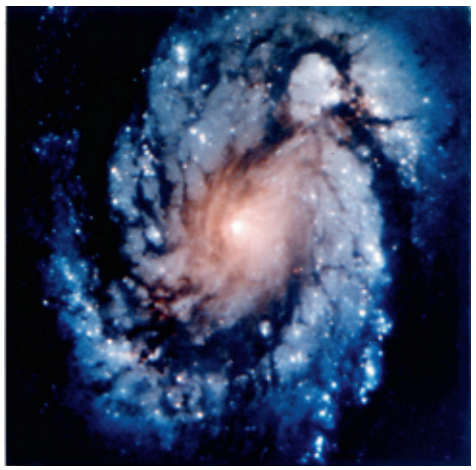
Wide field planetary camera 1

(a) **Before**



NASA Images

Wide field planetary camera 2

(b) **After correction**

Figure 3.33 (a) Image of a galaxy taken by the Hubble telescope before the lens was corrected. (b) The same galaxy after the lens was corrected.

in the chapter on color vision, has a visual pigment that absorbs light all the way down to 300 nm (see Figure 9.44, page 224). This very-short-wavelength pigment enables the honeybee to perceive ultraviolet wavelengths that are invisible to us, so the honeybee can see markings on flowers that reflect ultraviolet light (**Figure 3.34**). Thus, although perception does not *occur* in the eye, what we see is affected by what happens there. Similar effects occur in the other senses as well. Damage to the receptors in the ear is the main cause of hearing loss (Chapter 11, page 284); differences in the number of "bitter" receptors on people's tongues can cause two people to have different taste experiences to the same substance (Chapter 15, page 396).

(a)

Bjorn Rorslett

(b)

Figure 3.34 (a) A black-and-white photograph of a flower as seen by a human. (b) The same flower, showing markings that become visible to sensors that can detect ultraviolet light. Although we don't know exactly what honeybees see, their short-wavelength cone pigment makes it possible for them to sense these markings.

DEVELOPMENTAL DIMENSION Infant Visual Acuity

Most chapters in this book include "Developmental Dimensions," such as this one, which describe perceptual capacities of infants and young children that are related to material in the chapter.

One of the challenges of determining infant capacities is that infants can't respond by saying "yes, I perceive it" or "no, I don't perceive it" in reaction to a stimulus. But this difficulty has not stopped developmental psychologists from devising clever ways to determine what infants or young children are perceiving. One method that has been used to measure infant visual acuity is the **preferential looking (PL) technique**.

METHOD | Preferential Looking

The key to measuring infant perception is to pose the correct question. To understand what we mean by this, let's consider how we might determine infants' *visual acuity*, their ability to

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see details. To test adults, we can ask them to read the letters or symbols on an eye chart. But to test infant acuity, we have to ask another question and use another procedure. A question that works for infants is "Can you tell the difference between the stimulus on the left and the one on the right?" The way infants answer this question is by looking more at one of the stimuli.

In the preferential looking (PL) technique, two stimuli like the ones the infant is observing in **Figure 3.35** are presented, and the experimenter watches the infant's eyes to determine where the infant is looking. In order to guard against bias, the experimenter does not know which stimulus is being presented on the left or right. If the infant looks at one stimulus more than the other, the experimenter concludes that he or she can tell the difference between them.

The reason preferential looking works is that infants have *spontaneous looking preferences*; that is, they prefer to look at certain types of stimuli. For example, infants choose to look at objects with contours over ones that are homogeneous (Fantz et al., 1962). Thus, when we present a grating stimulus (alternating white and black bars like the one shown in Figure 3.35) with large bars on one side, and a gray field that reflects the same total amount of light that the grating would reflect on the other side (again, like the one shown in Figure 3.35), the infant can easily see the bars and therefore looks at the side with the bars more than the side with the gray field. If the infant looks preferentially at the side with the bars when the bars are switched randomly from side to side on different trials, he or she is telling the experimenter "I see the grating."

But decreasing the size of the bars makes it more difficult for the infant to tell the difference between the grating and gray stimulus. Eventually, the infant begins to look equally at each display, which tells the experimenter that very fine lines and the gray field are indiscriminable. Therefore, we can measure the infant's acuity by determining the narrowest stripe width that results in looking more at the grating stimulus.

Figure 3.35 An infant being tested using the preferential looking technique. The parent holds the infant in front of the display, which consists of a grating on the right and a homogeneous gray field on the left. The grating and the gray field have the same average light intensity. An experimenter, who does not know which side the grating is on in any given trial, looks through the peephole between the grating and the gray field and judges whether the infant is looking to the left or to the right.

How well can infants see details? The red curve in **Figure 3.36** shows acuity over the first year of life measured with the preferential looking technique, in which infants are tested with gratings, as in Figure 3.35. The blue curve indicates acuity determined by measuring an electrical signal called the **visual evoked potential** (VEP), which is recorded by disc electrodes placed on the infant's head over the visual part of the brain. For this technique, researchers alternate a gray field with a grating or checkerboard pattern. If the stripes or checks are large enough to be detected by the visual system, the visual system generates an electrical response called the *visual evoked potential*. If, however, the stripes are too fine to be detected by the visual system, no response is generated. Thus, the VEP provides an objective measure of the visual system's ability to detect details.

The VEP usually indicates better acuity than does preferential looking, but both techniques indicate that visual acuity is poorly developed at birth (about 20/400 to 20/600 at 1 month). (The expression 20/400 means that the infant must view a stimulus from 20 feet to see the same thing that an adult with normal

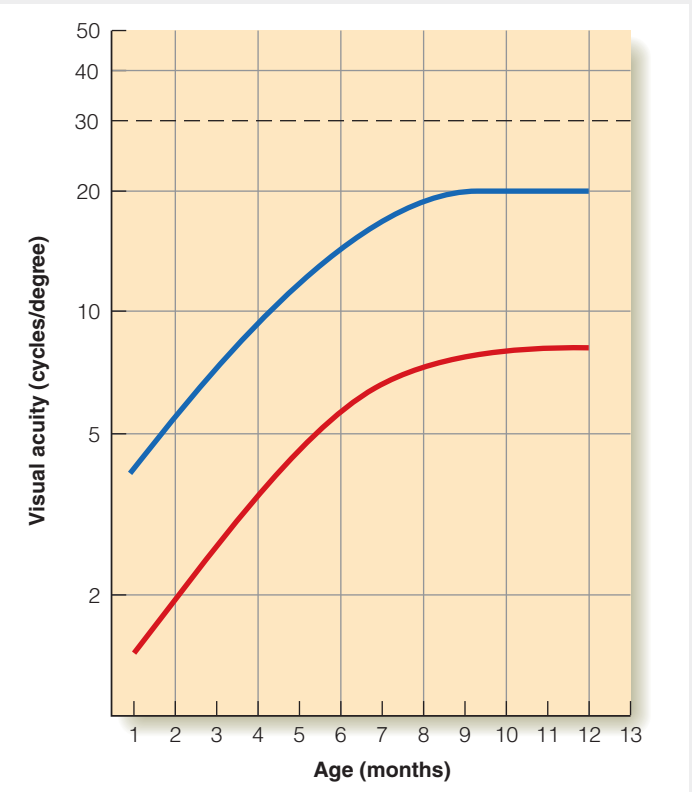

Figure 3.36 Acuity over the first year of life, measured by the visual evoked potential technique (top curve) and the preferential looking technique (bottom curve). The vertical axis indicates the fineness, in cycles per degree, of a grating stimulus that the infant can detect. One cycle per degree corresponds to one pair of black and white lines on a circle the size of a penny viewed from a distance of about a meter. Higher numbers indicate the ability to detect finer lines on the penny-sized circle. The dashed line is adult acuity (20/20 vision). (VEP curve adapted from Norcia & Tyler, 1985; PL curve adapted from Gwiazda et al., 1980, and Mayer et al., 1995.)

Continued

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vision can see from 400 feet.) Acuity increases rapidly over the first 6 to 9 months (Banks & Salapatek, 1978; Dobson & Teller, 1978; Harris et al., 1976; Salapatek et al., 1976). This rapid improvement of acuity is followed by a leveling-off period, and full adult acuity is not reached until sometime after 1 year of age.

From our discussion of how adult rod and cone visual acuity depends on the wiring of the rods and cones, it would make sense to consider the possibility that infants' low acuity might be traced to the development of their photoreceptors. If we look at the newborn's retina, we find that this is the case. Although the rod-dominated peripheral retina appears adultlike in the newborn, the all-cone fovea contains widely spaced and very poorly developed cone receptors (Abramov et al., 1982).

Figure 3.37a compares the shapes of newborn and adult foveal cones. Remember from our discussion of transduction that the visual pigments are contained in the receptor's outer segments. These outer segments sit on top of the other part of the receptor, the inner segment. The newborn's cones have fat inner segments and very small outer segments, whereas the adult's inner and outer segments are larger and are about the same diameter (Banks & Bennett, 1988; Yuodelis & Hendrickson, 1986). These differences in shape and size have a number of consequences. The small size of the outer segment means that the newborn's cones contain less visual pigment and therefore do not absorb light as effectively as adult cones. In addition, the fat inner segment creates the coarse receptor lattice shown in **Figure 3.37b**, with large spaces between the outer segments. In contrast, when the adult cones have become thin, they can become packed closely together to create a fine lattice that is well suited to detecting small details. Martin Banks and Patrick Bennett (1988) calculated that the cone receptors' outer segments effectively cover 68 percent of the adult fovea but only 2 percent of the newborn fovea. This means that most of the light entering the newborn's fovea is lost in the spaces between the cones and is therefore not useful for vision.

Thus, adults have good acuity because the cones have low convergence compared to the rods and the receptors in the fovea are packed closely together. In contrast, the infant's poor acuity can be traced to the fact that the infant's cones are spaced far apart. Another reason for the infant's poor acuity is that the visual area of the brain is poorly developed at birth, with fewer neurons and synapses than in the adult cortex. The rapid increase in acuity that occurs over the first 6 to 9 months of life can thus be traced to the fact that during that time, more neurons and synapses are being added to the cortex, and the infant's cones are becoming more densely packed.

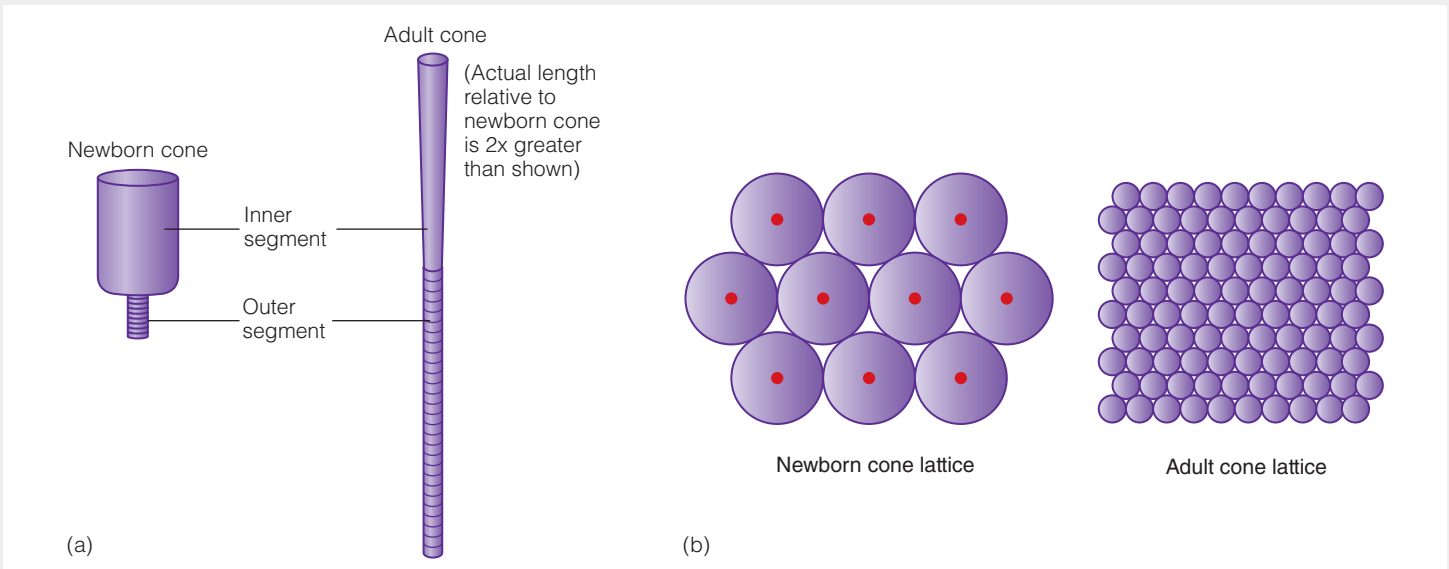

Figure 3.37 (a) Idealized shapes of newborn and adult foveal cones. (Real cones are not so perfectly straight and cylindrical.) Foveal cones are much narrower and longer than the cones elsewhere in the retina, so these look different from the one shown in Figure 3.3. (b) Receptor lattices for newborn and adult foveal cones. The newborn cone outer segments, indicated by the red circles, are widely spaced because of the fat inner segments. In contrast, the adult cones, with their slender inner segments, are packed closely together. (Adapted from Banks & Bennett, 1988)

TEST YOURSELF 3.2

1. What is convergence, and how can the differences in the convergence of rods and cones explain (a) the rods' greater sensitivity and (b) the cones' better detail vision?
2. What is a receptive field? What did Hartline's research indicate about receptive fields?
3. Describe the experiment that demonstrated the effect of lateral inhibition in the *Limulus*.
4. What is center-surround antagonism? Describe how lateral inhibition and convergence underlie center-surround antagonism.

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5. Discuss how lateral inhibition and center-surround receptive fields can lead to edge enhancement.
6. What is the Chevreul illusion? What does it illustrate about the difference between physical and perceptual?
7. What does it mean to say that early events are powerful shapers of perception? Give examples.
8. What is the young infant's visual acuity, and how does it change over the first year of life? What is the reason for (a) low acuity at birth and (b) the increase in acuity over the first 6 to 9 months?

THINK ABOUT IT

1. Ellen is looking at a tree. She sees the tree because light is reflected from the tree into her eyes, as shown in **Figure 3.38**. One way to describe this is to say that information about the tree is contained in the light. Meanwhile, Roger is off to the side, looking straight ahead. He doesn't see the tree because he is looking away from it. He is, however, looking right at the space through which the light that is carrying information from the tree to Ellen is passing. But Roger doesn't see any of this information. Why does this occur? (Hint #1: Consider the idea that "objects make light visible." Hint #2: Outer space contains a great deal of light, but it looks dark, except where there are objects.)
2. In the demonstration "Becoming Aware of What Is in Focus" on page 44, you saw that we see things clearly only when we are looking directly at them so that their image falls on the cone-rich fovea. But consider the common observation that the things we aren't looking at do not appear fuzzy, that the entire scene appears sharp or in focus. How can this be, in light of the results of the demonstration?
3. Here's an exercise you can do to get more in touch with the process of dark adaptation: Find a dark place where you can make some observations as you adapt to the dark. A closet is a good place to do this because you can regulate the intensity of light inside the closet by opening or closing the door. The idea is to create an environment in which there is dim light (no light at all is too dark). Take this book into the closet, opened to this page. (If you are reading an ebook on your device, make a paper copy of Figure 3.39 to take into the closet.) Close the closet door all the way, and then open the door slowly until you can just barely make out the white circle on the far left in **Figure 3.39** but can't see the others or see them as being very dim. As you sit in the dark, become aware that your sensitivity is increasing by noting how the circles to the right in the figure slowly become visible over a period of about 20 minutes. Also note that once a circle becomes visible, it gets easier to see as time passes. If you stare directly at the circles, they may fade, so move your eyes around every so often. Also, the circles will be easier to see if you look slightly above them.
4. Look for shadows, both inside and outside, and see if you can see Mach bands at the borders of the shadows. Remember that Mach bands are easier to see when the border of a shadow is slightly fuzzy. Mach bands are not actually present in the pattern of light and dark, so it is important to be sure that the bands are not really in the light but are created by the nervous system.

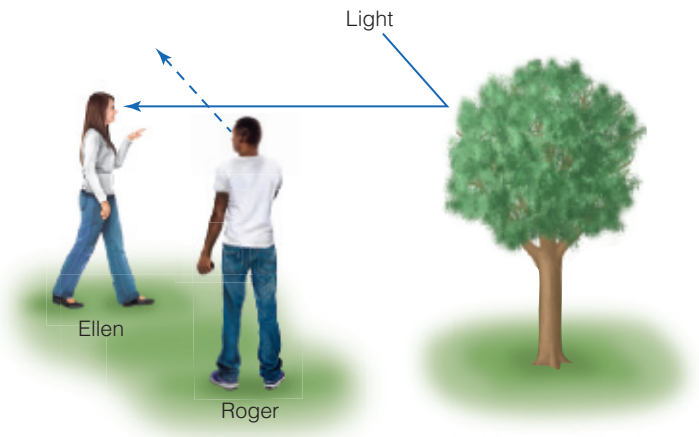

Figure 3.38 Ellen sees the tree because light is reflected from the tree into her eyes. Roger doesn't see the tree because he is not looking at it, but he is looking directly across the space where light from the tree is reflected into Ellen's eyes. Why isn't he aware of the information contained in this light?

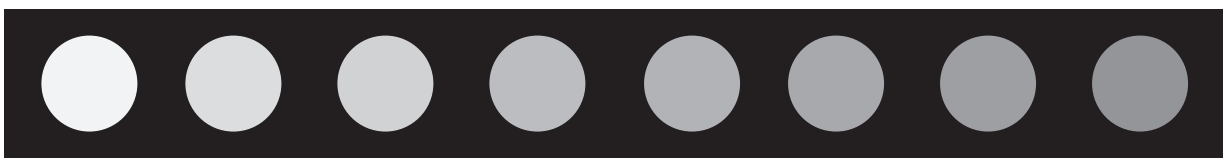

Figure 3.39 Dark adaptation test circles.

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KEY TERMS

Absorption spectrum (p. 50)
Accommodation (p. 43)
Amacrine cells (p. 52)
Axial myopia (p. 45)
Bipolar cells (p. 51)
Blind spot (p. 42)
Center-surround antagonism (p. 55)
Center-surround receptive field (p. 55)
Chevreul illusion (p. 58)
Cone spectral sensitivity (p. 49)
Cones (p. 41)
Convergence (p. 52)
Cornea (p. 40)
Dark adaptation (p. 46)
Dark adaptation curve (p. 46)
Dark-adapted sensitivity (p. 47)
Detached retina (p. 49)
Edge enhancement (p. 58)
Excitatory area (p. 56)
Excitatory-center, inhibitory-surround receptive field (p. 56)
Eyes (p. 40)
Farsightedness (p. 45)
Fovea (p. 41)
Ganglion cells (p. 51)
Horizontal cells (p. 52)
Hyperopia (p. 45)
Inhibitory area (p. 56)
Inhibitory-center, excitatory-surround receptive field (p. 56)
Isomerization (p. 46)
Lateral inhibition (p. 56)
Lens (p. 40)
Light-adapted sensitivity (p. 46)
Mach bands (p. 58)
Macular degeneration (p. 41)
Monochromatic light (p. 49)
Myopia (p. 45)
Nearsightedness (p. 45)
Neural circuits (p. 51)
Neural convergence (p. 52)
Ommatidia (p. 56)
Optic nerve (p. 41)
Outer segments (p. 41)
Peripheral retina (p. 41)
Photoreceptors (p. 40)
Preferential looking technique (p. 60)
Presbyopia (p. 45)
Pupil (p. 40)
Purkinje shift (p. 50)
Receptive field (p. 55)
Refractive errors (p. 44)
Refractive myopia (p. 45)
Retina (p. 40)
Retinitis pigmentosa (p. 42)
Rod monochromats (p. 48)
Rod–cone break (p. 48)
Rod spectral sensitivity curve (p. 49)
Rods (p. 40)
Spectral sensitivity (p. 49)
Spectral sensitivity curve (p. 49)
Transduction (p. 45)
Visible light (p. 40)
Visual acuity (p. 53)
Visual evoked potential (p. 61)
Visual pigment bleaching (p. 48)
Visual pigment regeneration (p. 49)
Visual pigments (p. 41)
Wavelength (p. 40)

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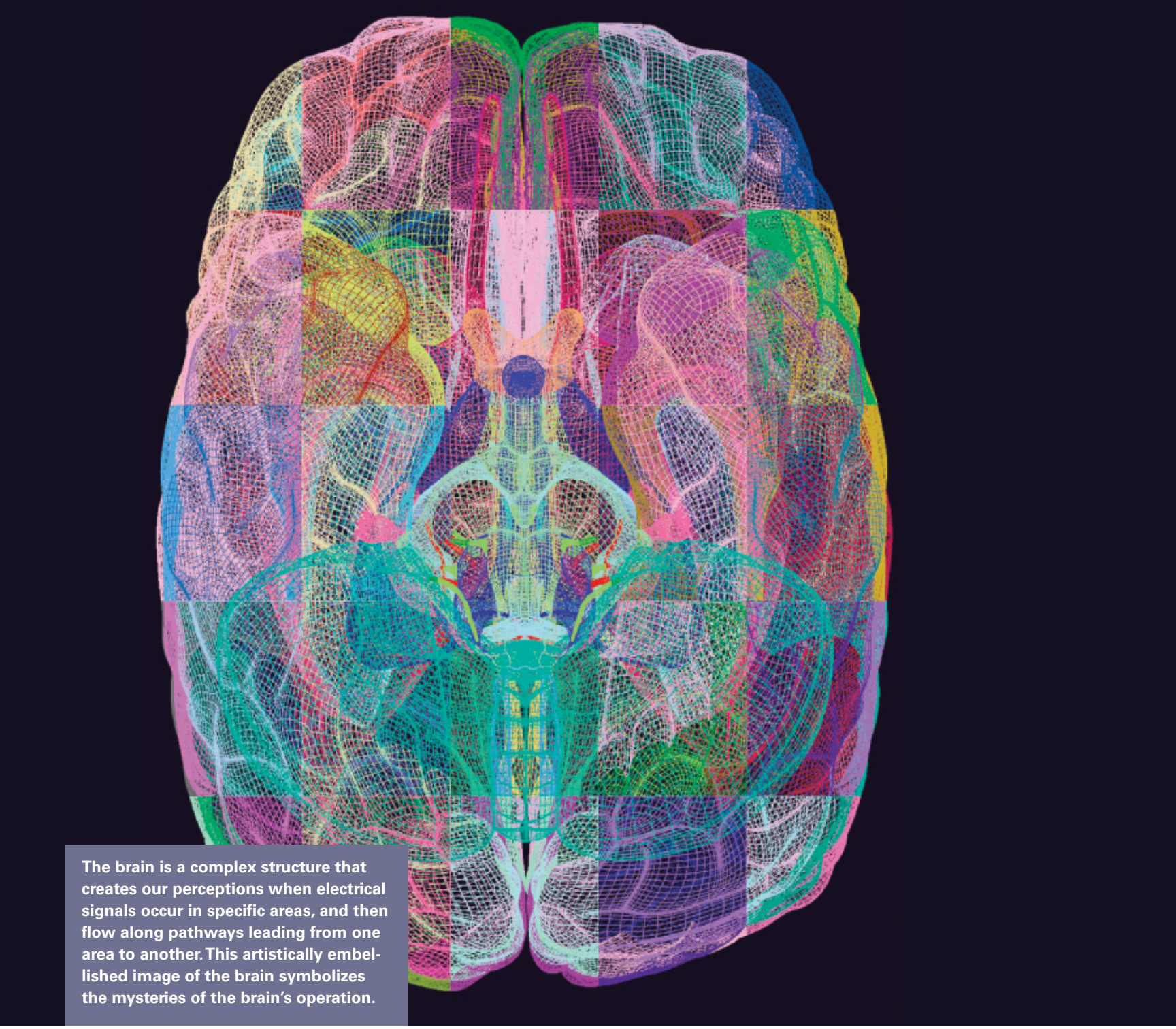

The brain is a complex structure that creates our perceptions when electrical signals occur in specific areas, and then flow along pathways leading from one area to another. This artistically embellished image of the brain symbolizes the mysteries of the brain's operation.

E. M. Pasieka/Science Photo Library/Corbis

Learning Objectives

After studying this chapter, you will be able to ...

- Explain how visual signals travel from the eye to the lateral geniculate nucleus, and then to the visual cortex.
- Distinguish between the different types of cells in the visual cortex and their role in perception.
- Describe experiments that illustrate the connection between neurons called "feature detectors" and perception.
- Discuss how perception of visual objects and scenes depends on neural "maps" and "columns" in the cortex.
- Describe visual pathways beyond the visual cortex, including the *what* and *where* streams and how the functions of these streams have been studied.
- Describe higher-level neurons, how they are involved in perceiving objects, and the connection between higher-level neurons and visual memories.
- Explain what is meant by "flexible" receptive fields.

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CHAPTER 4

The Visual Cortex and Beyond

CHAPTER CONTENTS

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TEST YOURSELF 4.2
THINK ABOUT IT

Some Questions We Will Consider:

- Where does the transduced visual signal go once it leaves the retina? (p. 68)
- How is visual information organized in the cortex? (p. 75)
- How do the responses of neurons change as we move higher in the visual system? (p. 79)

In Chapter 3, as we began our exploration of the perceptual process for vision, we saw that a number of transformations take place in the retina, before we get to the brain. Now we will focus our attention on the later stages of the visual process by looking at how electrical signals are sent from the eye to the visual cortex, what happens once they get there, and where they go next.

Historically, understanding functions of different parts of the brain often began with case studies of people with brain damage. Our knowledge of how the brain responds to visual input can be traced back to the Russo-Japanese War of 1904–1905. During this war, Japanese physician Tatsuji Inouye was treating soldiers who survived gunshot wounds to the head, and in doing so, he made an interesting observation. He noticed that if a soldier had a wound to the back of the head, his vision was impaired. And not only that, but the area of the head that was injured was correlated with the area of vision that was lost. For example, if the bullet wound was to the right side of the brain, then visual impairments were noticed on the left side of the soldier's visual field, and vice versa (Glickstein & Whitteridge, 1987).

While there was other early research on the brain's role in vision prior to Inouye's observations in humans (Colombo et al., 2002), his contributions spoke not only to function (that the back of the brain is involved in vision), but also to organization (that the location in the brain maps onto the location in the visual field).

4.1 From Retina to Visual Cortex

How does the visual signal get from the retina to the visual area of the cortex? And once it has reached the cortex, how is it processed?

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Pathway to the Brain

The pathway from the retina to the brain is illustrated in **Figure 4.1**. The first thing that happens on this journey is that the visual signals from both eyes leave the back of the eye in the optic nerve and meet at a location called the **optic chiasm**. The optic chiasm is an x-shaped bundle of fibers on the underside of the brain. Interestingly, if you were to hold a human brain and flip it over, you could actually see the optic chiasm.

At the optic chiasm, some of the fibers cross to the opposite side of the brain from the eye they came from. The result of this crossing is that all fibers corresponding to the right visual field, regardless of eye, end up on the left side—or hemisphere—of the brain, and vice versa. In this way, each hemisphere of the brain responds to the opposite, or **contralateral**, side of the visual field. This can be seen in the color coding in **Figure 4.1b**. The visual field is determined based on where the person is fixating; anything to right of the point of central focus is the right visual field (processed by the left hemisphere), and anything to the left is the left visual field (processed by the right hemisphere). Importantly, both eyes can see both visual fields. You can determine this for yourself by holding up your finger and looking directly at it, and noticing that you can still see to the left and right of your finger even if you close your left or right eye.

After meeting at the optic chiasm and crossing to the contralateral hemisphere, the visual signal's journey to the cortex continues. Approximately 90 percent of the signals from the retina proceed to the **lateral geniculate nucleus (LGN)**, located in the thalamus of each hemisphere, while the other 10 percent of fibers travel to the **superior colliculus** (Figure 4.1b), a structure involved in controlling eye movements. In vision and in other senses as well, the thalamus serves as a relay station where incoming sensory information often makes a stop before reaching the cerebral cortex.

In Chapter 3, we introduced receptive fields and showed that ganglion cells receptive fields have a center-surround organization (Kuffler, 1953). As it turns out, neurons in the LGN also have center-surround receptive fields (Hubel & Wiesel, 1961). The fact that little change occurred in receptive fields when moving from the retina to the LGN made researchers wonder about the function of the LGN.

One proposal of LGN function is based on the observation that the signal sent from the LGN to the cortex is smaller than the input the LGN receives from the retina (**Figure 4.2**). This decrease in the signal leaving the LGN has led to the suggestion that one of the purposes of the LGN is to regulate neural information as it flows from the retina to the cortex (Casagrande & Norton, 1991; Humphrey & Saul, 1994).

Another important characteristic of the LGN is that it receives more signals from the cortex than from the retina (Sherman & Koch, 1986; Wilson et al., 1984). This "backward" flow of information, called *feedback*, could also be involved in

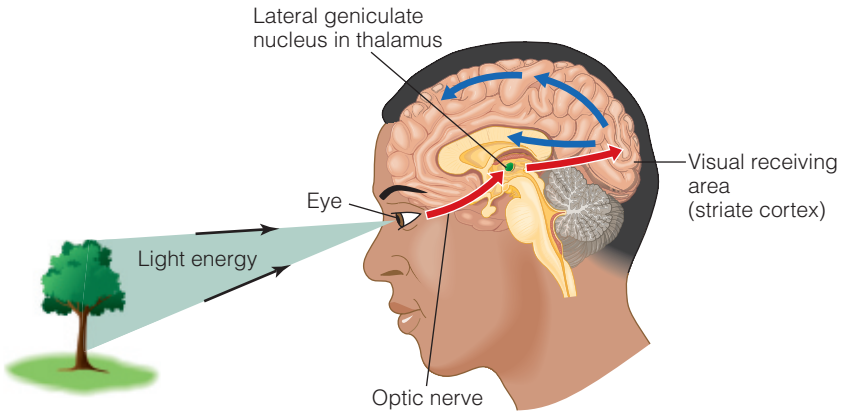

Figure 4.1 (a) Side view of the visual system, showing the major sites along the primary visual pathway where processing takes place: the eye, the optic nerve, the lateral geniculate nucleus, and the visual receiving area of the cortex. (b) Visual system seen on the underside of the brain, showing the superior colliculus, which receives some of the signals from the eye. The optic chiasm is the place where some of the fibers from each eye cross over to the other side of the brain, so they reach the contralateral (opposite) hemisphere of the visual cortex. This is illustrated by the colors, with red indicating fibers transmitting information about the right visual field and blue indicating fibers transmitting information about the left visual field.

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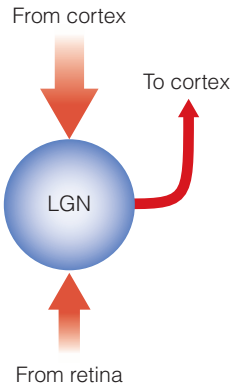

Figure 4.2 Information flow into and out of the LGN. The sizes of the arrows indicate the sizes of the signals.

regulation of information flow, the idea being that the information the LGN receives back from the brain may play a role in determining which information is sent up to the brain. As we will see later in the book, there is good evidence for the role of feedback in perception (Gilbert & Li, 2013).

From the LGN, the visual signal then travels to the *occipital lobe*, which is the **visual receiving area**—the place where signals from the retina and LGN first reach the cortex. The visual receiving area is also called the **striate cortex**, because it has a striped appearance when viewed in cross section, or **area V1** to indicate that it is the first visual area in the cortex. As indicated by the blue arrows in **Figure 4.1a**, signals also travel to other places in the cortex—a fact that we will return to later in this chapter.

We have seen how the signals leaving the eye cross at the optic chiasm, make a stop in the LGN, and then proceed to the visual cortex. Next, we'll see how neurons in the visual cortex respond to those incoming signals.

Receptive Fields of Neurons in the Visual Cortex

Our discussion of receptive fields in Chapter 3 focused on the center-surround receptive fields of ganglion cells. Once the concept of receptive fields was introduced, researchers realized that they could follow the effects of processing through different levels of the visual system by determining which patterns of light are most effective in generating a response in neurons at each level. This was the strategy adopted by David Hubel and Thorsten Wiesel, who made substantial contributions to the study of receptive fields. In fact, their work was so important to the field that it earned them the Nobel Prize in Physiology and Medicine in 1981. Hubel and Wiesel (1965) state their tactic for understanding receptive fields as follows:

> One approach ... is to stimulate the retina with patterns of light while recording from single cells or fibers at various points along the visual pathway. For each cell, the optimum stimulus can be determined, and one can note the characteristics common to cells at each level in the visual pathway, and compare a given level with the next. (Hubel & Wiesel, 1965, p. 229)

In their study of receptive fields, Hubel and Wiesel (1965) modified earlier procedures that were used to present light to the retina. Instead of shining light directly into the animal's eye, Hubel and Wiesel had animals look at a screen on which they projected stimuli.

METHOD | Presenting Stimuli to Determine Receptive Fields

A neuron's receptive field is determined by presenting a stimulus, such as a spot of light, to different places on the retina to determine which areas result in no response, an excitatory response, or an inhibitory response. Hubel and Wiesel projected stimuli onto a screen (**Figure 4.3**). The animal, usually a cat or monkey, was anesthetized and looked at the screen, its eyes focused with glasses so that whatever was presented on the screen would be in focus on the back of the eye.

Because the cat's eye remains stationary, each point on the screen corresponds to a point on the cat's retina. Thus, a stimulus at point A on the screen creates an image on point A on the retina, B creates an image on B, and C on C. There are many advantages to projecting an image on a screen. Stimuli are easier to control compared to projecting light directly into the eye (especially for moving stimuli); they are sharper; and it is easier to present complex stimuli such as faces or scenes.

An important thing to remember about receptive fields, which is always true no matter what method is used, is that *the receptive field is always on the receptor surface*. The receptor surface is the retina in our examples, but as we will see later, there are also receptive fields in the touch system on the surface of the skin. It is also important to note that it doesn't matter where the *neuron* is—the neuron can be in the retina, the cortex serving vision or touch, or elsewhere in the brain, but the receptive field is always on the receptor surface, because that is where the stimuli are *received*.

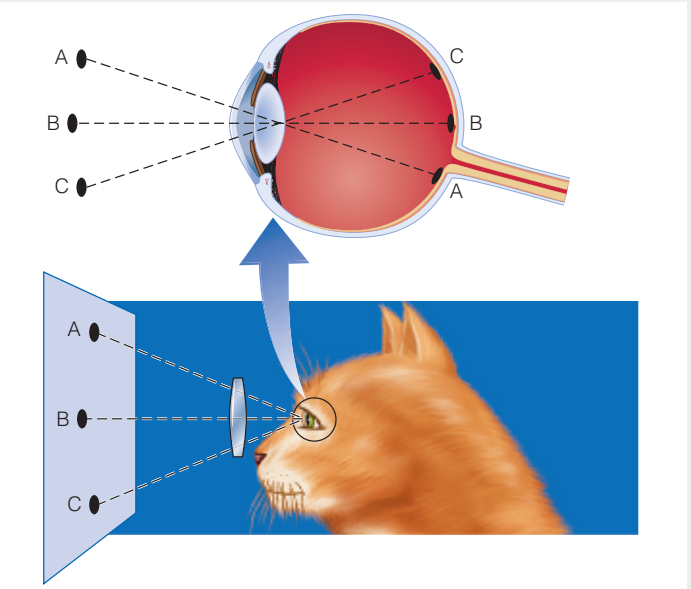

Figure 4.3 Method of determining receptive fields using a projection screen to present the stimuli. Each location on the projection screen corresponds to a location on the retina. Receptive fields can be recorded from neurons anywhere in the visual system, but the receptive field is always located on the retina.

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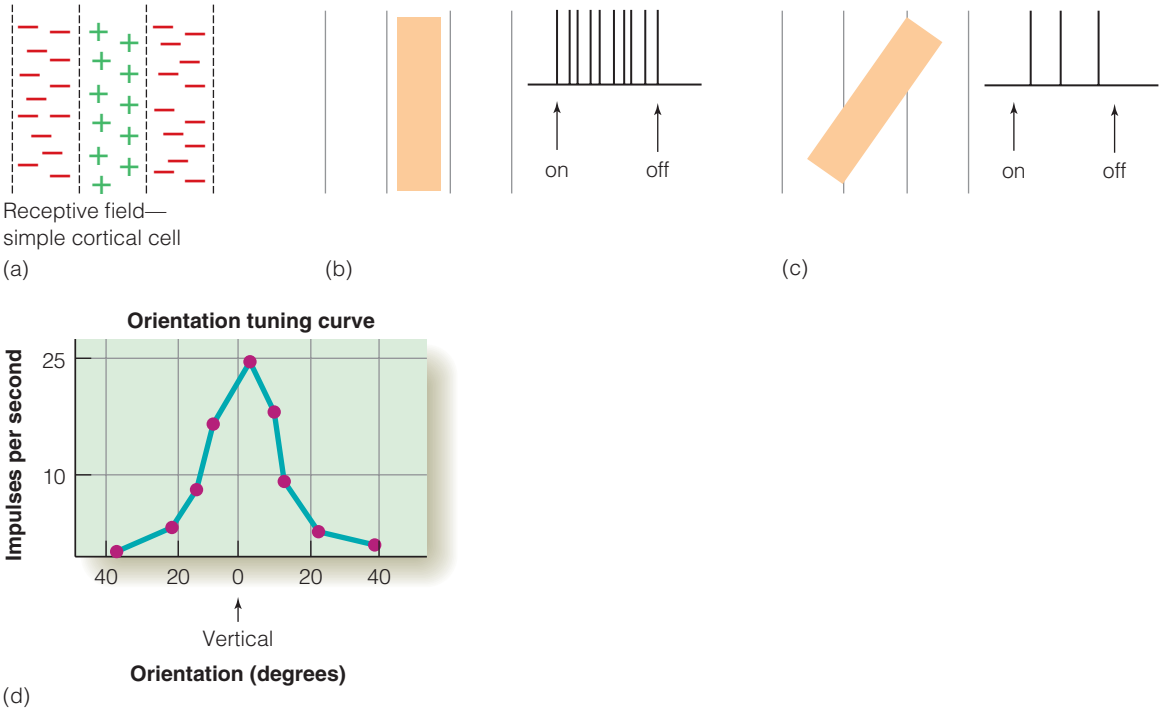

Figure 4.4 (a) An example of a receptive field of a simple cortical cell. (b) This cell responds best to a vertical bar of light that covers the excitatory area of the receptive field. (c) The response decreases as the bar is tilted so that it also covers the inhibitory area. (d) Orientation tuning curve of a simple cortical cell for a neuron that responds best to a vertical bar (orientation = 0).

By flashing spots of light on different places in the retina, Hubel and Wiesel found cells in the striate cortex with receptive fields that, like center-surround receptive fields of neurons in the retina and LGN, have excitatory and inhibitory areas. However, these areas are arranged side by side rather than in the center-surround configuration (**Figure 4.4a**). Cells with these side-by-side receptive fields are called simple cortical cells.

We can tell from the layout of the excitatory and inhibitory areas of the simple cell shown in Figure 4.4a that a cell with this receptive field would respond best to a vertical bar of light, line, or edge. Hubel and Wiesel found that not only do the simple cells respond to bars, but to bars of particular orientations. As shown in **Figure 4.4b**, a vertical bar that illuminates only the excitatory area causes high firing, but as the bar is tilted so the inhibitory area is illuminated, firing decreases (**Figure 4.4c**).

The relationship between orientation and firing is indicated by a neuron's orientation tuning curve, which is determined by measuring the responses of a simple cortical cell to bars with different orientations. The tuning curve in **Figure 4.4d** shows that the cell responds with 25 nerve impulses per second to a vertically oriented bar and that the cell's response decreases as the bar is tilted away from the vertical and begins stimulating inhibitory areas of the neuron's receptive field. Notice that a bar tilted 20 degrees from the vertical elicits only a small response. This particular simple cell responds best to a bar with a vertical orientation (in other words, it "prefers" vertically oriented bars), but there are other simple cells in the visual cortex that respond to other orientations, so there are neurons that respond to all of the orientations that exist in the environment.

Although Hubel and Wiesel were able to use small spots of light to map the receptive fields of simple cortical cells like the one in Figure 4.4, they found that many of the cells they encountered in the striate cortex and nearby visual areas did not respond to small spots of light. In his Nobel lecture, Hubel described how he and Wiesel were becoming increasingly frustrated in their attempts to get these neurons to fire, when something startling happened: As they inserted a glass slide containing a spot stimulus into their slide projector,[1] a visual cortex neuron "went off like a machine gun" (Hubel, 1982). The neuron, as it turned out, was responding not to the spot at the center of the slide that Hubel and Wiesel had planned to use as a stimulus, but to the image of the slide's edge moving downward on the screen as the slide dropped into the projector (**Figure 4.5**). Upon realizing this, Hubel and Wiesel changed their stimuli from small spots to moving lines and were then able to find cells that responded to oriented moving bars. As with simple cells, a particular neuron had a preferred orientation.

Hubel and Wiesel (1965) discovered that many cortical neurons respond best to moving barlike stimuli with specific orientations. Complex cells, like simple cells, respond best to

[1]A slide projector is a device that, until the advent of digital technology, was the method of choice for projecting images onto a screen. Slides were inserted into the projector and the images on the slides were projected onto the screen. Although slides and slide projectors have been replaced by digital imaging devices, it is still possible to purchase slide projectors on the Internet; however, the popular Kodachrome slide film used to shoot family vacation pictures was discontinued in 2009.

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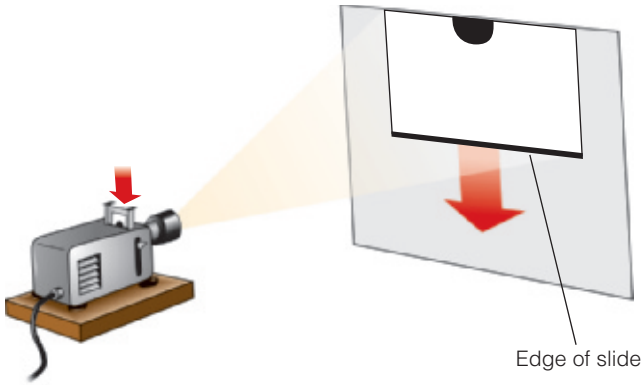

Figure 4.5 When Hubel and Wiesel dropped a slide into their slide projector, the image of the edge of the slide moving down unexpectedly triggered activity in a visual cortex neuron.

bars of a particular orientation. However, unlike simple cells, which respond to small spots of light or to stationary stimuli, most complex cells respond only when a correctly oriented bar of light moves across the entire receptive field. Further, many complex cells respond best to a particular direction of movement (**Figure 4.6a**). Because these neurons don't respond to stationary flashes of light, their receptive fields are indicated not by pluses and minuses but by outlining the area that, when stimulated, elicits a response in the neuron.

Another type of cell in the visual cortex, called **end-stopped cells**, fires to moving lines of a specific length or to moving corners or angles. **Figure 4.6b** shows a light corner stimulus that is being moved up and down across the retina. The records to the right indicate that the neuron responds best to a medium-sized corner that is moving upward.

Hubel and Wiesel's finding that some neurons in the visual cortex respond only to oriented lines and others respond best to corners was an extremely important discovery because it extended the idea first proposed in connection with center-surround receptive fields that neurons respond to some patterns of light and not to others. This makes sense because the purpose of the visual system is to enable us to perceive objects in the environment, and many objects can be at least crudely represented by simple shapes and lines of various orientations. Thus, Hubel and Wiesel's discovery that neurons respond selectively to oriented lines and stimuli with specific lengths was an important step toward determining how neurons respond to more complex objects.

Table 4.1, which summarizes the properties of the neurons we have described so far, illustrates an important fact about neurons in the visual system: As we travel farther from the retina, neurons fire to more complex stimuli. Retinal ganglion cells respond best to spots of light, whereas cortical end-stopped cells respond best to bars of a certain length that are moving in a particular direction. Because simple, complex, and end-stopped cells fire in response to specific features of the stimulus, such as orientation or direction of movement, they have also been called **feature detectors**. Next, we will discuss how these feature detectors in the visual cortex are important to perception.

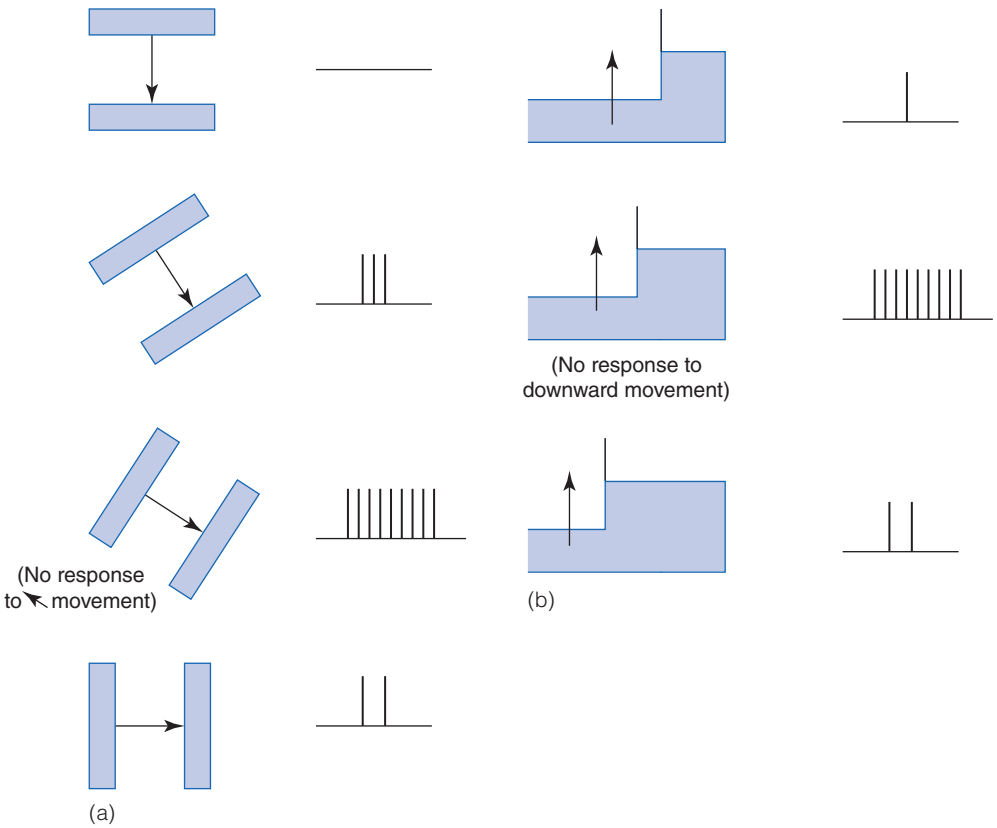

Figure 4.6 (a) Response of a complex cell recorded from the visual cortex of the cat. The stimulus bar is moved back and forth across the receptive field. This cell fires best when the bar is positioned with a specific orientation and is moved from left to right. (b) Response of an end-stopped cell recorded from the visual cortex of the cat. The stimulus is indicated by the light area on the left. This cell responds best to a medium-sized corner that is moving up.

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Table 4.1 Properties of Neurons in the Retina, LGN, and Visual Cortex

TYPE OF CELL	CHARACTERISTICS OF RECEPTIVE FIELD
Ganglion cell	Center-surround receptive field. Responds best to small spots, but will also respond to other stimuli.
Lateral geniculate	Center-surround receptive fields very similar to the receptive field of a ganglion cell.
Simple cortical	Excitatory and inhibitory areas arranged side by side. Responds best to bars of a particular orientation.
Complex cortical	Responds best to movement of a correctly oriented bar across the receptive field. Many cells respond best to a particular direction of movement.
End-stopped cortical	Responds to corners, angles, or bars of a particular length moving in a particular direction.

4.2 The Role of Feature Detectors in Perception

Neural processing endows neurons in the visual cortex with properties that make them feature detectors that respond best to a specific type of stimulus. When researchers show that neurons respond to oriented lines, they are measuring the *stimulus–physiology relationship* (arrow B in **Figure 4.7**), introduced in Chapter 1. But just measuring this relationship does not prove that these neurons have anything to do with the perception of oriented lines. To demonstrate a link between physiology and perception, it is necessary to measure the *physiology–behavior relationship* (arrow C). One way this has been accomplished is by using a psychophysical procedure called *selective adaptation*.

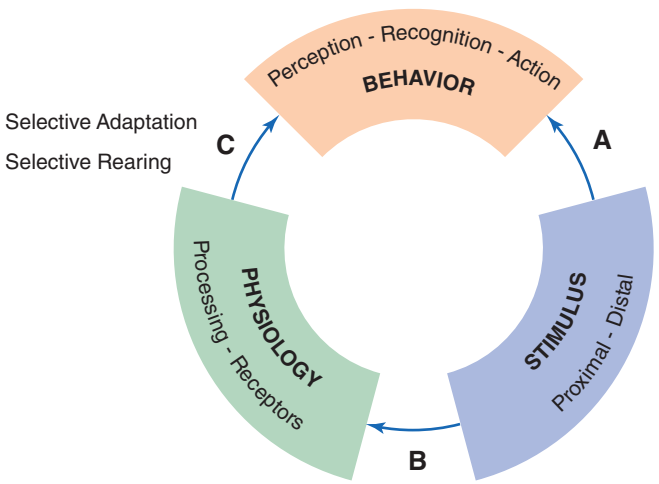

Figure 4.7 Three-part version of the perceptual process, repeated from **Figure 1.13**, showing the three basic relationships: (A) stimulus–behavior, (B) stimulus–physiology, and (C) physiology–behavior. "Selective Adaptation" and "Selective Rearing" refer to experiments described in the text that were designed to measure relationship C.

Selective Adaptation

When we view a stimulus with a specific property, neurons tuned to that property fire. The idea behind **selective adaptation** is that this firing causes neurons to eventually become fatigued, or adapt. This adaptation causes two physiological effects: (1) the neuron's firing rate decreases, and (2) the neuron fires less when that stimulus is immediately presented again. According to this idea, presenting a vertical line causes neurons that respond to vertical lines to respond, but as these presentations continue, these neurons eventually begin to fire less to vertical lines. Adaptation is *selective* because only the neurons that were responding to verticals or near-verticals adapt, and neurons that were not firing do not adapt.

METHOD Psychophysical Measurement of the Effect of Selective Adaptation to Orientation

Measuring the effect of selective adaptation to orientation involves the following three steps:

1. Measure a person's *contrast threshold* to gratings with a number of different orientations (**Figure 4.8a**). A grating's contrast threshold is the minimum intensity difference between two adjacent bars that can just be detected. The contrast threshold for seeing a grating is measured by changing the intensity difference between the light and dark bars until the bars can just barely be seen. For example, it is easy to see the four gratings on the left of **Figure 4.9**, because the difference in intensity between the bars is above threshold. However, there is only a small intensity difference between the bars of the grating on the far right, so it is close to the contrast threshold. The intensity difference at which the bars can just barely be seen is the contrast threshold.
2. Adapt the person to one orientation by having the person view a high-contrast *adapting stimulus* for a minute or two. In this example, the *adapting stimulus* is a vertical grating (**Figure 4.8b**).
3. Remeasure the contrast threshold of all the test stimuli presented in step 1 (**Figure 4.8c**).

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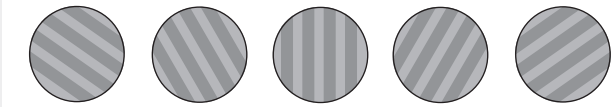
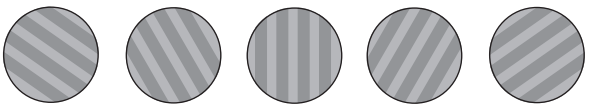


(a) Measure contrast threshold at a number of orientations.

(b) Adapt to a high-contrast grating.



(c) Remeasure contrast thresholds for same orientations as above.

Figure 4.8 Procedure for carrying out a selective adaptation experiment. See text for details.

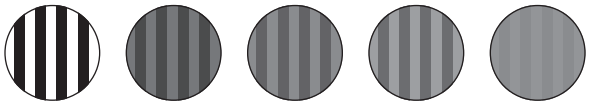


Figure 4.9 The contrast threshold for a grating is the minimum difference in intensity at which the observer can just make out the bars. The grating on the left is far above the contrast threshold. The ones in the middle have less contrast but are still above threshold. The grating on the far right is near the contrast threshold. (From Womelsdorf et al., 2006)

The rationale behind this procedure is that if the adaptation to the high-contrast grating in step 2 decreases the functioning of neurons that determine the perception of verticals, this should cause an increase in contrast threshold so it is more difficult to see low-contrast vertical gratings. In other words, adapting vertical feature detectors should make it necessary to increase the difference between the black and white vertical bars in order to see them. **Figure 4.10a** shows that this is exactly what happens. The peak of the contrast threshold curve, which indicates that a large increase in the difference between the bars was needed to see the bars, occurs at the vertical adapting orientation.

The important result of this experiment is that our psychophysical curve shows that adaptation selectively affects only some orientations, just as neurons selectively respond to only some orientations. In fact, comparing the psychophysically determined selective adaptation curve (Figure 4.10a) to the orientation tuning curve for a simple cortical neuron (**Figure 4.10b**) reveals that they are very similar. (The psychophysical curve is slightly wider because the adapting stimulus affects some neurons that respond to orientations near the adapting orientation.)

The near match between the orientation selectivity of neurons and the perceptual effect of selective adaptation supports the idea that feature detectors—in this case, simple cells in the visual cortex—play a role in perception. The selective adaptation experiment is measuring how a physiological effect (adapting the feature detectors that respond to a specific orientation) causes a perceptual result (decrease in sensitivity to that orientation). This evidence that feature detectors have something to do with perception means that when you look at a complex scene, such as a city street or a crowded shopping mall, feature detectors that are firing to the orientations in the scene are helping to construct your perception of the scene.

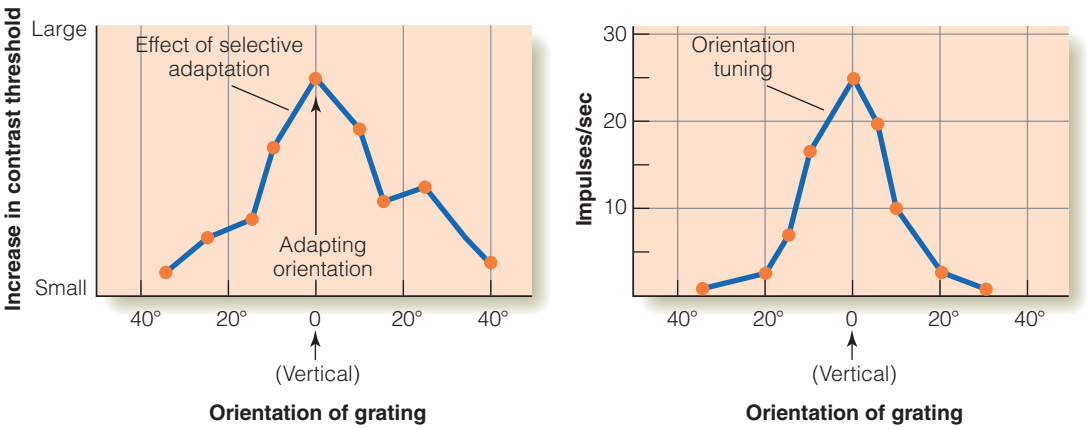


Figure 4.10 (a) Results of a psychophysical selective adaptation experiment. This graph shows that the person's adaptation to the vertical grating causes a large decrease in the ability to detect the vertical grating when it is presented again but has less effect on gratings that are tilted to either side of the vertical. (b) Orientation tuning curve of the simple cortical neuron from Figure 4.4.

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Selective Rearing

Further evidence that feature detectors in the visual cortex are involved in perception is provided by **selective rearing** experiments. The idea behind selective rearing is that if an animal is reared in an environment that contains only certain types of stimuli, then neurons that respond to these stimuli will become more prevalent. This follows from a phenomenon called **neural plasticity** or **experience-dependent plasticity**—the idea that the response properties of neurons can be shaped by perceptual experience. According to this idea, rearing an animal in an environment that contains only vertical lines should result in the animal's visual cortex having simple cells that respond predominantly to verticals.

This result may seem to contradict the results of the selective adaptation experiment just described, in which exposure to verticals *decreases* the response to verticals. However, adaptation is a short-term effect. Presenting the adapting orientation for a few minutes decreases responding to that orientation. In contrast, selective rearing is a longer-term effect. Presenting the rearing orientation over a period of days or even weeks keeps the neurons that respond to that orientation active. Meanwhile, neurons that respond to orientations that aren't present are not active, so they lose their ability to respond to those orientations.

One way to describe the results of selective rearing experiments is "Use it or lose it." This effect was demonstrated in a classic experiment by Colin Blakemore and Grahame Cooper (1970) in which they placed kittens in striped tubes like the one in **Figure 4.11a**, so that each kitten was exposed to only one orientation, either vertical or horizontal. The kittens were kept in the dark from birth to 2 weeks of age, at which time they were placed in the tube for 5 hours a day; the rest of the time they remained in the dark. Because the kittens sat on a Plexiglas platform, and the tube extended both above and below them, there were no visible corners or edges in their environment other than the stripes on the sides of the tube. The kittens wore cones around their head to prevent them from seeing vertical stripes as oblique or horizontal stripes by tilting their heads; however, according to Blakemore and Cooper, "The kittens did not seem upset by the monotony of their surroundings and they sat for long periods inspecting the walls of the tube" (p. 477).

When the kittens' behavior was tested after 5 months of selective rearing, they seemed blind to the orientations that they hadn't seen in the tube. For example, a kitten that was reared in an environment of vertical stripes would pay attention to a vertical rod but ignore a horizontal rod. Following behavioral testing, Blakemore and Cooper recorded from simple cells in the visual cortex and determined the stimulus orientation that caused the largest response from each cell.

Figure 4.11b shows the results of this experiment. Each line indicates the orientation preferred by a single neuron in the cat's cortex. This cat, which was reared in a vertical environment, has many neurons that respond best to vertical or near-vertical stimuli, but none that respond to horizontal stimuli. The horizontally responding neurons were apparently lost because they hadn't been used. The opposite result occurred for the horizontally reared cats. The parallel between the orientation selectivity of neurons in the cat's cortex and the cat's

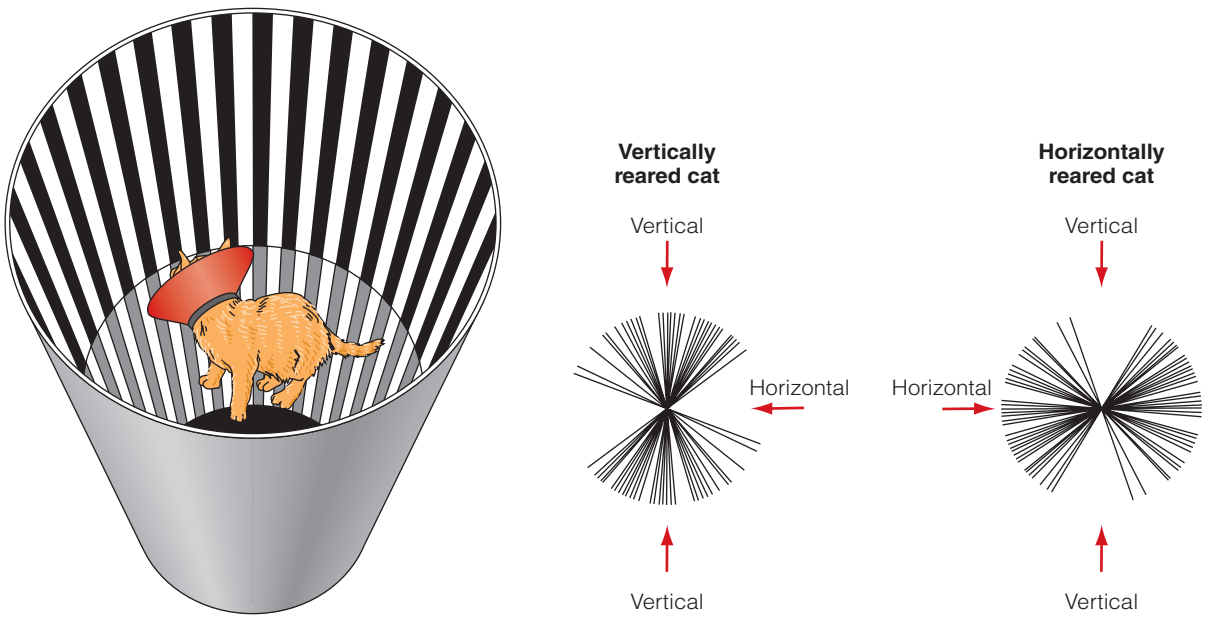

Figure 4.11 (a) Striped tube used in Blakemore and Cooper's (1970) selective rearing experiments. (b) Distribution of optimal orientations for 72 simple cells from a cat reared in an environment of vertical stripes, on the left, and for 52 simple cells from a cat reared in an environment of horizontal stripes, on the right.
(Blakemore & Cooper, 1970)

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behavioral response to the same orientation provides more evidence that feature detectors are involved in the perception of orientation. This connection between feature detectors and perception was one of the major discoveries of vision research in the 1960s and 1970s.

Related to this result is the oblique effect discussed in Chapter 1 (p. 12)—the fact that people perceive vertical and horizontal lines better than slanted lines. What is important about the oblique effect is not only that people see horizontals and verticals better, but that the brain's response to detecting horizontals and verticals is larger than when detecting slanted lines (Figure 1.16, page 14). Possibly, just as the orientation selectivity of the kitten's neurons matched its horizontal or vertical environment, the response of human neurons reflects the fact that horizontals and verticals are more common than slanted lines in our environment (Coppola et al., 1998).

So far, we have seen how visual cortex neurons fire in response to certain features, like specific orientations of lines that comprise edges of objects in our visual world. We've also seen how these "feature detectors" are related to perception, as demonstrated in the selective adaptation and selective rearing experiments. We now consider how these neurons are organized in the visual cortex.

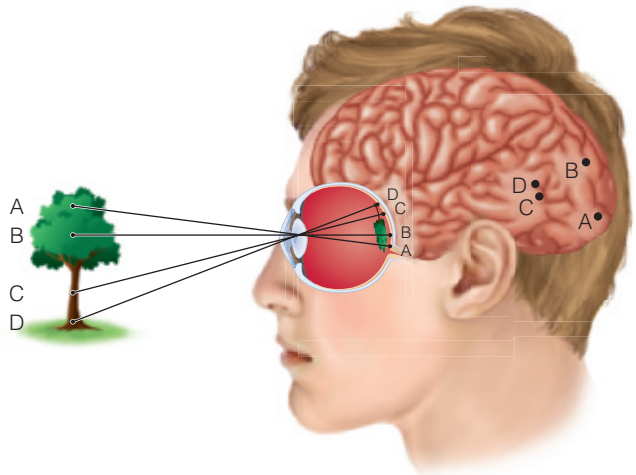

Figure 4.12 A person looking at a tree, showing how points A, B, C, and D are imaged on the retina and where these retinal activations cause activity in the brain. Although the distances between A and B and between C and D are about the same on the retina, the distance between A and B is much greater on the cortex. This is an example of cortical magnification, in which more space is devoted to areas of the retina near the fovea.

4.3 Spatial Organization in the Visual Cortex

When we look out at a scene, things are organized across our visual field. There's a house on the left, a tree next to the house, and a car parked in the driveway on the other side of the house. This organization of objects in visual space becomes transformed into organization in the eye, when an image of the scene is created on the retina. It is easy to appreciate spatial organization at the level of the retinal image because this image is essentially a picture of the scene. But once the house, the tree, and the car have been transformed into electrical signals, the signals created by each object then become organized in the form of "neural maps," so that objects that create images near each other on the retina are represented by neural signals that are near each other in the cortex.

The Neural Map in the Striate Cortex (V1)

To begin describing neural maps, let's describe how points in the retinal image are represented *spatially* in the striate cortex (area V1). We determine this by stimulating various places on the retina and noting where neurons fire in the cortex. **Figure 4.12** shows a man looking at a tree so that points A, B, C, and D on the tree stimulate points A, B, C, and D on his retina. Moving to the cortex, the image at point A on the retina causes neurons at point A to fire in the cortex. The image at point B causes neurons at point B to fire, and so on. This example shows how points on the retinal image cause activity in the cortex.

This example also shows that locations on the cortex correspond to locations on the retina. This electronic map of the retina on the cortex is called a **retinotopic map**. This organized spatial map means that two points that are close together on an object and on the retina will activate neurons that are close together in the brain (Silver & Kastner, 2009).

But let's look at this retinotopic map a little more closely, because it has a very interesting property that is relevant to perception. Although points A, B, C, and D in the cortex correspond to points A, B, C, and D on the retina, you might notice something about the *spacing* of these locations. Considering the retina, we note that the man is looking at the leaves at the top of the tree, so points A and B are both near the fovea and the images of points C and D at the bottom of the trunk are in the peripheral retina. But although A and B and C and D are the same distance apart on the retina, the spacing is not the same on the cortex. A and B are farther apart on the cortex than C and D. What this means is that electrical signals associated with the part of the tree near where the person is looking are allotted more space on the cortex than signals associated with parts of the tree that are located off to the side—in the periphery. In other words, the spatial representation of the visual scene on the cortex is distorted, with more space being allotted to locations near the fovea than to locations in the peripheral retina.

Even though the fovea accounts for only 0.01 percent of the retina's area, signals from the fovea account for 8 to 10 percent of the retinotopic map on the cortex (Van Essen & Anderson, 1995). This apportioning of a large area on the cortex to the small fovea is called **cortical magnification**. The size of this magnification, which is called the **cortical magnification factor**, is depicted in **Figure 4.13**.

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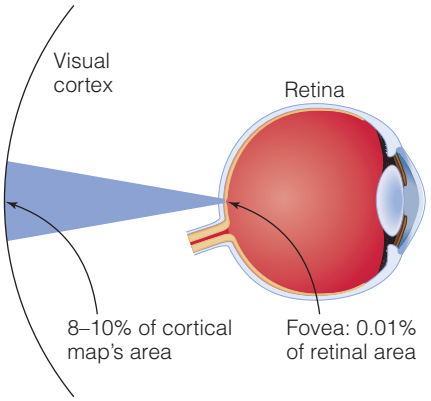

Figure 4.13 The magnification factor in the visual system. The small area of the fovea is represented by a large area on the visual cortex.

Cortical magnification has been determined in the human cortex using brain imaging (see Chapter 2, page 31). Robert Dougherty and coworkers (2003) had participants in the fMRI scanner look at stimuli like the one shown in **Figure 4.14a**. The participant looked directly at the center of the screen, so the dot at the center fell on the fovea. During the experiment, stimulus light was presented in two places: (1) near the center (red area), which illuminated a small area near the fovea; and (2) farther from the center (blue area), which illuminated an area in the peripheral retina. The areas of the visual cortex activated by these two stimuli are indicated in **Figure 4.14b**. This activation illustrates cortical magnification because stimulation of the small area near the fovea activated a greater area on the cortex (red) than stimulation of the larger area in the periphery (blue). (Also see Wandell, 2011.)

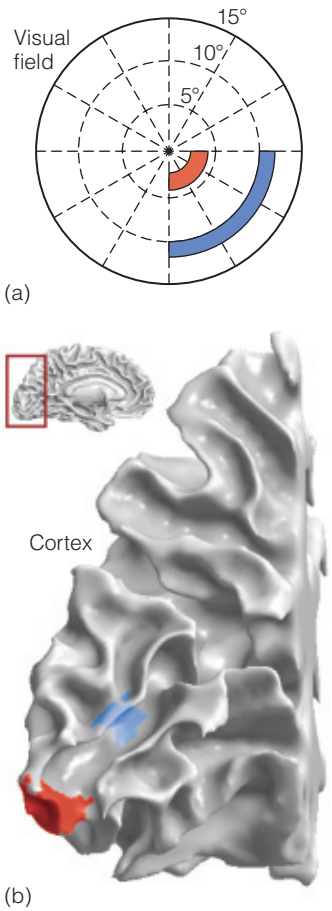

Figure 4.14 (a) Red and blue areas show the extent of stimuli that were presented while a person was in an fMRI scanner. (b) Red and blue indicate areas of the brain activated by the stimulation in (a). (From Dougherty et al., 2003)

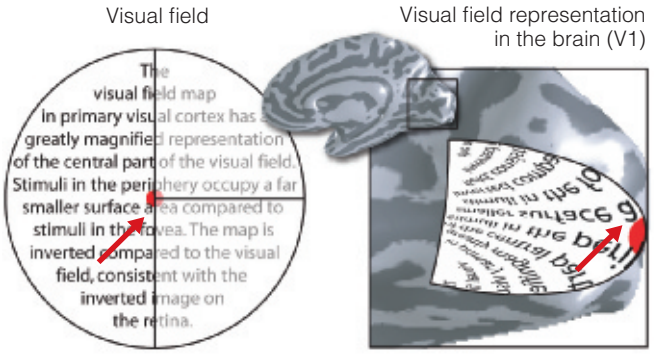
Visual field
Visual field representation in the brain (V1)
The visual field map in primary visual cortex has a greatly magnified representation of the central part of the visual field. Stimuli in the periphery occupy a far smaller surface area compared to stimuli in the fovea. The map is inverted compared to the visual field, consistent with the inverted image on the retina.

Figure 4.15 Demonstration of the magnification factor. A person looks at the red spot on the text on the left. The area of brain activated by each letter of the text is shown on the right. The arrows point to the letter *a* in the text on the left, and the area in the brain activated by the *a* on the right. (Based on Wandell et al., 2009)

The large representation of the fovea in the cortex is also illustrated in **Figure 4.15**, which shows the space that would be allotted to words on a page (Wandell et al., 2009). Notice that the letter "a," which is near where the person is looking (red arrow), is represented by a much larger area in the cortex than letters that are far from where the person is looking. The extra cortical space allotted to letters and words at which the person is looking provides the extra neural processing needed to accomplish tasks such as reading that require high visual acuity (Azzopardi & Cowey, 1993).

What cortical magnification means when you look at a scene is that information about the part of the scene you are looking at takes up a larger space on your visual cortex than an area of equal size that is off to the side. Another way to appreciate the magnification factor is to do the following demonstration.

DEMONSTRATION | Cortical Magnification of Your Finger

Hold your left hand at arm's length, holding your index finger up. As you look at your finger, hold your right hand at arm's length, about a foot to the right of your finger and positioned so the back of your hand is facing you. When you have done this, your left index finger (which you are still looking at) activates an area of cortex as large as the area activated by your whole right hand.

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An important thing to note about this demonstration is that even though the image of your finger on the fovea takes up about the same space on the cortex as the image of your hand on the peripheral retina, you do not perceive your finger as being as *large* as your hand. Instead, you see the *details* of your finger far better than you can see details on your hand. That more space on the cortex translates into better detailed vision rather than larger size is an example of the fact that what we perceive doesn't exactly match the "picture" in the brain. We will return to this idea shortly.

The Cortex Is Organized in Columns

We determined the retinotopic map on the brain by measuring activity near the surface of the cortex. We are now going to consider what is happening below the surface by looking at the results of experiments in which a recording electrode was inserted into the visual cortex.

Location and Orientation Columns Hubel and Wiesel (1965) carried out a series of experiments in which they recorded from neurons they encountered as they lowered electrodes into the visual cortex. When they inserted an electrode perpendicular to the surface of a cat's cortex, they found that every neuron they encountered had its receptive field at about the same location on the retina. Their results are shown in **Figure 4.16a**, which shows four neurons along the electrode track, and **Figure 4.16b**, which shows that these neurons' receptive fields are all located at about the same place on the retina. From this result, Hubel and Wiesel concluded that the striate cortex is organized into location columns that are perpendicular to the surface of the cortex, so that all of the neurons within a location column have their receptive fields at the same location on the retina.

As Hubel and Wiesel lowered their electrodes perpendicular to the surface of the cortex, they noted not only that the

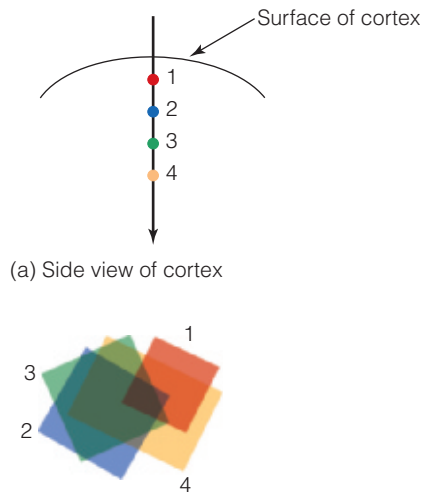

Figure 4.16 Location column in the visual cortex. When an electrode penetrates the cortex perpendicularly, the receptive fields of the neurons encountered along this track overlap. The receptive field recorded at each numbered position along the electrode track (a) is indicated by a correspondingly numbered square (b).

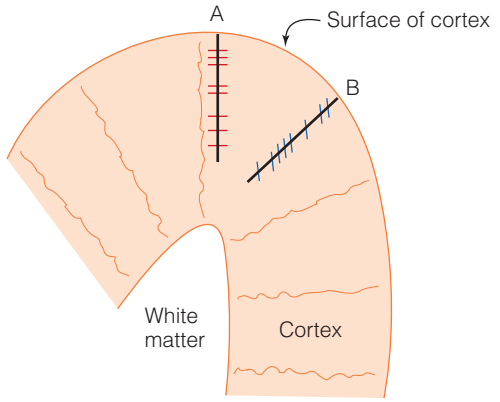

Figure 4.17 Orientation columns in the visual cortex. All of the cortical neurons encountered along track A respond best to horizontal bars (indicated by the red lines cutting across the electrode track). All of the neurons along track B respond best to bars oriented at 45 degrees.

neurons along this track had receptive fields with the same *location* on the retina, but that these neurons all preferred stimuli with the same *orientation*. Thus, all cells encountered along the electrode track at A in **Figure 4.17** fired the most to horizontal lines, whereas all those along electrode track B fired the most to lines oriented at about 45 degrees. Based on this result, Hubel and Wiesel concluded that the cortex is also organized into orientation columns, with each column containing cells that respond best to a particular orientation.

Hubel and Wiesel also showed that adjacent orientation columns have cells with slightly different preferred orientations. When they moved an electrode through the cortex obliquely (not perpendicular to the surface), so that the electrode cut across orientation columns, they found that the neurons' preferred orientations changed in an orderly fashion, so a column of cells that respond best to 90 degrees is right next to the column of cells that respond best to 85 degrees (**Figure 4.18**). Hubel and Wiesel also found that as they moved

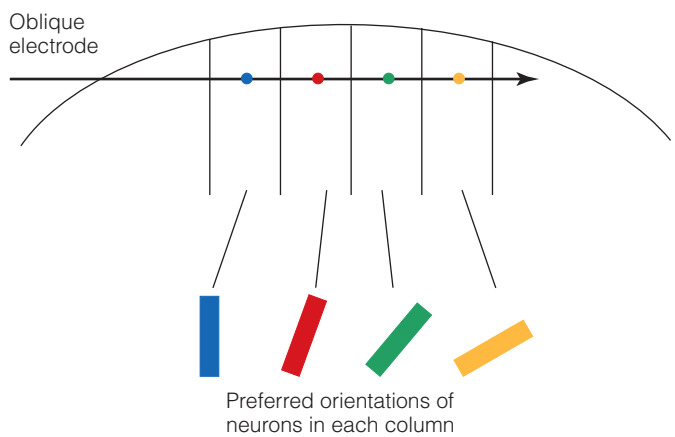

Figure 4.18 If an electrode is inserted obliquely into the visual cortex, it crosses a sequence of orientation columns. The preferred orientation of neurons in each column, indicated by the bars, changes in an orderly way as the electrode crosses the columns. The distance the electrode is advanced is exaggerated in this illustration.

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their electrode 1 millimeter across the cortex, their electrode passed through orientation columns that represented the entire range of orientations. Interestingly enough, this 1-mm dimension is the size of one location column.

One Location Column: Many Orientation Columns

This 1-mm dimension for location columns means that one location column is large enough to contain orientation columns that cover all possible orientations. Thus, the location column shown in **Figure 4.19** serves one location on the retina (all the neurons in the column have their receptive fields at about the same place on the retina) *and* contains neurons that respond to all possible orientations.

Think about what this means. Neurons in that location column receive signals from a particular location on the retina, which corresponds to a small area in the visual field. Because this location column contains some neurons that respond to every possible orientation, any oriented edge or line that falls within the location column's area on the retina will be able to be represented by some of the neurons in this location column.

A location column with all of its orientation columns was called a **hypercolumn** by Hubel and Wiesel. A hypercolumn receives information about all possible orientations that fall within a small area of the retina; it is therefore well suited for processing information from a small area in the visual field.[2]

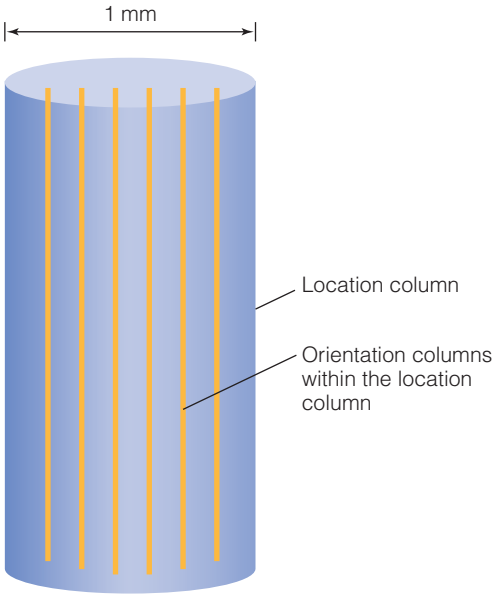

Figure 4.19 A location column that contains the full range of orientation columns. A column such as this, which Hubel and Wiesel called a *hypercolumn*, receives information about all possible orientations that fall within a small area of the retina.

[2]In addition to location and orientation columns, Hubel and Wiesel also described *ocular dominance columns*. Most neurons respond better to one eye than to the other. This preferential response to one eye is called *ocular dominance*, and neurons with the same ocular dominance are organized into ocular dominance columns in the cortex. This means that each neuron encountered along a perpendicular electrode track responds best to either the left eye or the right eye. There are two ocular dominance columns within each hypercolumn, one for the left eye and one for the right.

How V1 Neurons and Columns Underlie Perception of a Scene

Now that we've discussed visual cortex neurons, what they respond to, and how they are organized into columns, let's put it all together to understand how these processes are involved in our perception of a visual scene.

Determining how the millions of neurons in the cortex respond when we look at a scene such as the one in **Figure 4.20a** is an ambitious undertaking. We will simplify the task by focusing on one small part of the scene—the tree trunk in **Figure 4.20b**. We focus specifically on the part of the trunk shown passing through the three circles, A, B, and C.

Figure 4.21a shows how the image of this part of the tree trunk is projected onto the retina. Each circle represents the area served by a location column. **Figure 4.21b** shows the location columns in the cortex. Remember that each of these location columns contains a complete set of orientation columns (Figure 4.19). This means that the vertical tree trunk will activate neurons in the 90-degree orientation columns in each location column, as indicated by the orange areas in each column.

Thus, the continuous tree trunk is represented by the firing of neurons sensitive to a specific orientation in a number of separate columns in the cortex. Although it may be a bit surprising that the tree is represented by separate columns in the cortex, it simply confirms a property of our perceptual system that we mentioned earlier: The cortical representation of a stimulus does not have to *resemble* the stimulus; it just has to contain information that *represents* the stimulus. The representation of the tree in the visual cortex is contained in the firings of neurons in separate cortical columns. As we'll soon discuss, at some point in the cortex, the information in these separated columns must be combined to create our perception of the tree.

Before leaving our description of how objects are represented by neural activity in the visual cortex, let's return to our scene (**Figure 4.22**). Each circle or ellipse in the scene

(a) (b)

Figure 4.20 (a) A scene from the Pennsylvania woods. (b) Focusing in on part of a tree trunk. A, B, and C represent the parts of the tree trunk that fall on receptive fields in three areas of the retina.

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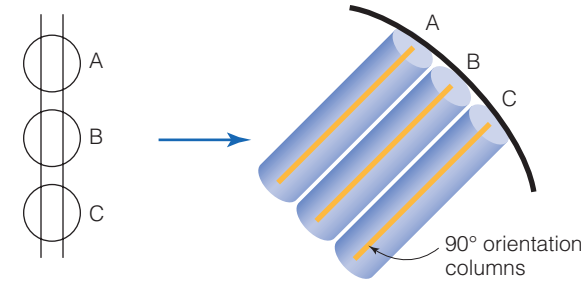

Figure 4.21 (a) Receptive fields A, B, and C, located on the retina, for the three sections of the tree trunk from Figure 4.20b. The neurons associated with each of these receptive fields are in different location columns. (b) Three location columns in the cortex. Neurons that fire to the tree trunk's orientation are within the orange areas of the location column.

represents an area that sends information to one location column. Working together, these columns cover the entire visual field, an effect called **tiling**. Just as a wall can be covered by adjacent tiles, the visual field is served by adjacent (and often overlapping) location columns (Nassi & Callaway, 2009). (Does this sound familiar? Remember the football field analogy for ganglion cell receptive fields on page 55 of Chapter 3, in which each spectator was observing a small area of the field. In that example, the spectators were *tiling* the football field.)

The idea that each part of a scene is represented by activity in many location columns means that a scene containing many objects is represented in the striate cortex by an amazingly complex pattern of firing. Just imagine the process we described for the three small areas on the tree trunk multiplied by hundreds or thousands. Of course, this representation in the striate cortex is only the first step in representing the tree. As we will now see, signals from the striate cortex travel to a number of other places in the cortex for further processing.

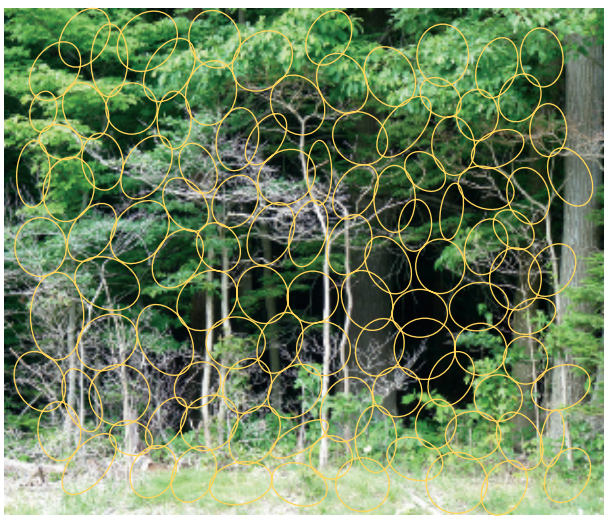

Figure 4.22 The yellow circles and ellipses superimposed on the forest scene each represent an area that sends information to one location column in the visual cortex. There are actually many more columns than shown here, and they overlap, so that they cover the entire scene. The way these location columns cover the entire scene is called *tiling*.

TEST YOURSELF 4.1

1. Describe the pathway from the retina to the brain. What does it mean when we say that the visual system has a contralateral organization?
2. What function has been suggested for the LGN? How are LGN receptive fields similar to ganglion cell receptive fields?
3. Describe the characteristics of simple, complex, and end-stopped cells in the visual cortex. Why have these cells been called feature detectors?
4. How has the psychophysical procedure of selective adaptation been used to demonstrate a link between feature detectors and the perception of orientation? Be sure you understand the rationale behind a selective adaptation experiment and also how we can draw conclusions about physiology from the results of this psychophysical procedure.
5. How has the procedure of selective rearing been used to demonstrate a link between feature detectors and perception? Be sure you understand the concept of neural plasticity.
6. How is the retina mapped onto the striate cortex? What is cortical magnification, and what function does it serve?
7. Describe location columns and orientation columns. What do we mean when we say that location columns and orientation columns are "combined"? What is a hypercolumn?
8. How do V1 neurons and columns underlie perception of a scene? Start by describing how a tree trunk is represented in the cortex and then expand your view to the whole forest scene.

4.4 Beyond the Visual Cortex

At this point, we have discussed how the visual signal travels from the retina to the visual cortex, and how those V1 neurons represent the basic elements or features of the visual scene (edges and lines). Now, we will discuss what happens to these signals as they progress through the visual system.

After being processed in the striate cortex (V1), the visual signal proceeds to other visual areas in the occipital lobe and beyond—areas conveniently known as V2, V3, V4, and V5 (**Figure 4.23**). These areas collectively are often referred to as the **extrastriate cortex**, since they are outside of the striate cortex.

As we move from V1 to higher-level extrastriate areas, the receptive field sizes gradually increase. V1 neurons respond to a very small area of the retina (which corresponds to a very small area of the visual field); their receptive fields, as we have seen,

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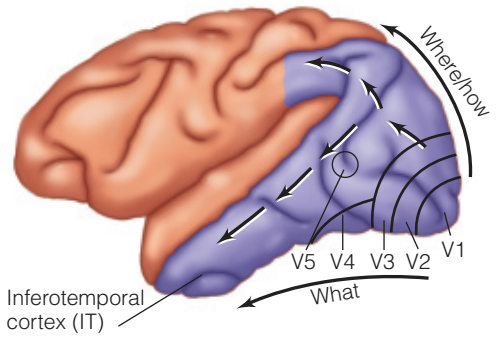

Figure 4.23 The hierarchy of cortical areas and pathways in the visual system. The visual signal flows from striate cortex (area V1) at the back of the brain to extrastriate cortex (areas V2–V5) through the *what* (ventral) and *where/how* (dorsal) pathways.

are just large enough to encompass a line or an edge. V2 neuron receptive fields are slightly larger, V3 even larger, and so on (Smith et al., 2001). In this way, the representation of the visual scene builds as we move up this hierarchy of extrastriate cortex areas, adding more and more aspects of the visual scene such as corners, colors, motion, and even entire shapes and objects.

When the visual signal leaves the occipital lobe, it continues through different "streams" or pathways that serve different functions. Some of the first research on these pathways was carried out by Leslie Ungerleider and Mortimer Mishkin, who presented evidence for two streams serving different functions that transmit information from the striate and extrastriate cortex to other areas of the brain.

Streams for Information About What and Where

Ungerleider and Mishkin (1982) used a technique called *ablation* (also called *lesioning*) to better understand the functional organization of the visual system. Ablation refers to the destruction or removal of tissue in the nervous system.

METHOD | **Brain Ablation**

The goal of a brain ablation experiment is to determine the function of a particular area of the brain. First, an animal's ability to carry out a specific task is determined by behavioral testing. Most ablation experiments have used monkeys because of the similarity of their visual system to that of humans and because monkeys can be trained in ways that enable researchers to determine perceptual capacities such as acuity, color vision, depth perception, and object perception (Mishkin et al., 1983).

Once the animal's performance on a task has been measured, a particular area of the brain is ablated (removed or destroyed), either by surgery or by injecting a chemical that destroys tissue near the place where it is injected. Ideally, one particular area is removed and the rest of the brain remains intact. After ablation, the monkey is retested to determine how performance has been affected by the ablation.

Ungerleider and Mishkin presented monkeys with two tasks: (1) an object discrimination problem and (2) a landmark discrimination problem. In the **object discrimination problem**, a monkey was shown one object, such as a rectangular solid, and was then presented with a two-choice task like the one shown in **Figure 4.24a**, which included the "target" object (the rectangular solid) and another stimulus, such as the triangular solid. If the monkey was able to discriminate between the two objects and thus push aside the target object, it received the food reward that was hidden in a well under the object. The **landmark discrimination problem** is shown in **Figure 4.24b**. Here, the monkey's task was to remove the cover of the food well that was closest to the "landmark"—in this case, a tall cylinder.

In the ablation part of the experiment, part of the temporal lobe was removed in some monkeys. After ablation, behavioral testing showed that the object discrimination problem was very difficult for these monkeys. This result indicates that the pathway that reaches the temporal lobes is responsible for determining an object's *identity*. Ungerleider and Mishkin therefore called the pathway leading from the striate cortex to the temporal lobe the ***what* pathway** (Figure 4.23).

Other monkeys had their parietal lobes removed, as in Figure 4.24b, and they had difficulty solving the landmark discrimination problem. This result indicates that the pathway that leads to the parietal lobe is responsible for determining an object's *location*. Ungerleider and Mishkin therefore called the

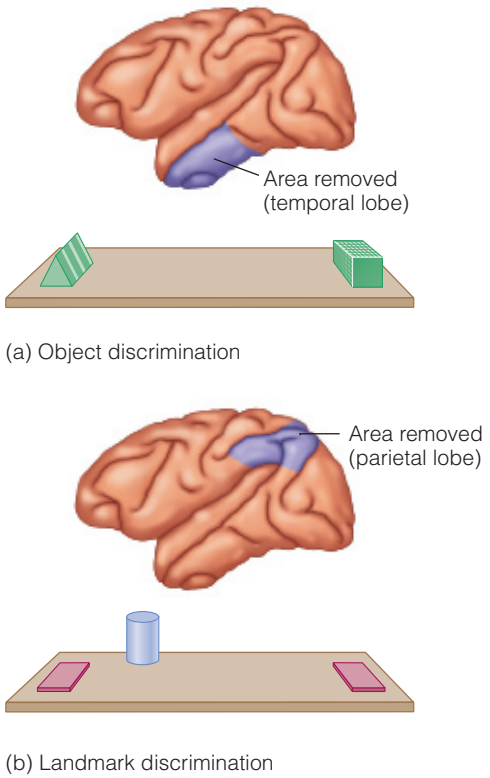

Figure 4.24 The two types of discrimination tasks used by Ungerleider and Mishkin. (a) Object discrimination: Pick the correct shape. Lesioning the temporal lobe (shaded area) makes this task difficult. (b) Landmark discrimination: Pick the food well closer to the cylinder. Lesioning the parietal lobe makes this task difficult. (From Mishkin et al., 1983)

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pathway leading from the striate cortex to the parietal lobe the ***where* pathway** (Figure 4.23).

The *what* and *where* pathways are also called the **ventral pathway** (what) and the **dorsal pathway** (where), because the lower part of the brain, where the temporal lobe is located, is the ventral part of the brain, and the upper part of the brain, where the parietal lobe is located, is the dorsal part of the brain. The term *dorsal* refers to the back or the upper surface of an organism; thus, the dorsal fin of a shark or dolphin is the fin on the back that sticks out of the water. **Figure 4.25** shows that for upright, walking animals such as humans, the dorsal part of the brain is the top of the brain. (Picture a person with a dorsal fin sticking out of the top of his or her head!) *Ventral* is the opposite of dorsal; hence it refers to the lower part of the brain.

The discovery of two pathways in the cortex—one for identifying objects (what) and one for locating objects (where)—led some researchers to look back at the retina and the lateral geniculate nucleus (LGN). Using the techniques of both recording from neurons and ablation, they found that properties of the ventral and dorsal streams are established by two different types of ganglion cells in the retina, which transmit signals to different layers of the LGN (Schiller et al., 1990). Thus, the cortical ventral and dorsal streams can actually be traced back to the retina and LGN.

Although there is good evidence that the ventral and dorsal pathways serve different functions, it is important to note that (1) the pathways are not totally separated but have connections between them and (2) signals flow not only "up" the pathway from the occipital lobe toward the parietal and temporal lobes but "back" as well (Gilbert & Li, 2013; Merigan & Maunsell, 1993; Ungerleider & Haxby, 1994). It makes sense that there would be communication between the pathways because in our everyday behavior we need to both identify and locate objects, and we routinely coordinate these two activities every time we identify something ("there's a pen") and notice where it is ("it's over there, next to the computer"). Thus, there are two distinct pathways, but some information is shared between them. The "backward" flow of information, called *feedback*, provides information from higher centers that can influence the signals flowing into the system (Gilbert & Li, 2013). This feedback is one of the mechanisms behind top-down processing, introduced in Chapter 1 (p. 10).

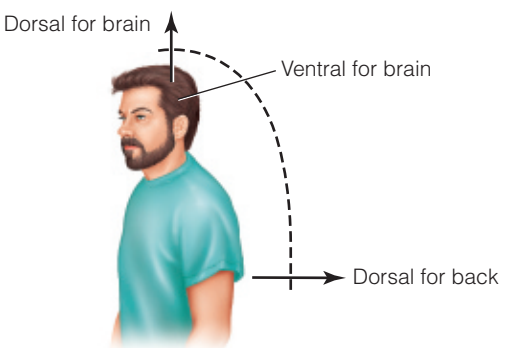

Figure 4.25 *Dorsal* refers to the back surface of an organism. In upright standing animals such as humans, dorsal refers to the back of the body *and* to the top of the head, as indicated by the arrows and the curved dashed line. Ventral is the opposite of dorsal.

Streams for Information About *What* and *How*

Although the idea of ventral and dorsal streams has been generally accepted, David Milner and Melvyn Goodale (1995; see also Goodale & Humphrey, 1998, 2001) have suggested that the dorsal stream does more than just indicate where an object is. Milner and Goodale propose that the dorsal stream is for taking action, such as picking up an object. Taking this action would involve knowing the location of the object, consistent with the idea of *where*, but it goes beyond *where* to involve a physical interaction with the object. Thus, reaching to pick up a pen involves information about the pen's location *plus* information about how a person should move his or her hand toward the pen. According to this idea, the dorsal stream provides information about *how* to direct action with regard to a stimulus.

Evidence supporting the idea that the dorsal stream is involved in how to direct action is provided by the discovery of neurons in the parietal cortex that respond (1) when a monkey looks at an object and (2) when it reaches toward the object (Sakata et al., 1992; also see Taira et al., 1990). But the most dramatic evidence supporting the idea of a dorsal *how* or *action* stream comes from neuropsychology—the study of the behavioral effects of brain damage in humans (see Chapter 2, page 31).

METHOD | Double Dissociations in Neuropsychology

One of the basic principles of neuropsychology is that we can understand the effects of brain damage by determining double dissociations, which involve two people: In one person, damage to one area of the brain causes function A to be absent while function B is present; in the other person, damage to another area of the brain causes function B to be absent while function A is present.

Ungerleider and Mishkin's monkeys provide an example of a double dissociation. The monkey with damage to the temporal lobe was unable to discriminate objects (function A) but had the ability to solve the landmark problem (function B). The monkey with damage to the parietal lobe was unable to solve the landmark problem (function B) but was able to discriminate objects (function A). These two findings, taken together, are an example of a double dissociation. The fact that object discrimination and the landmark task can be disrupted separately and in opposite ways means that these two functions operate independently of one another.

An example of a double dissociation in humans is provided by two hypothetical patients. Alice, who has suffered damage to her temporal lobe, has difficulty naming objects but has no trouble indicating where they are located (**Table 4.2a**). Bert, who has parietal lobe damage, has the opposite problem—he can identify objects but can't tell exactly where they are located (**Table 4.2b**). The cases of Alice and Bert, taken together, represent a double dissociation and enable us to conclude that recognizing objects and locating objects operate independently of each other.

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Table 4.2 A Double Dissociation

	ABLE TO NAME OBJECTS?	ABLE TO DETERMINE OBJECT'S LOCATION?
(a) ALICE: Temporal lobe damage (ventral stream)	NO	YES
(b) BERT: Parietal lobe damage (dorsal stream)	YES	NO

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The Behavior of Patient D.F. Milner and Goodale (1995) used the method of determining double dissociations to study D.F., a 34-year-old woman who suffered damage to her ventral pathway from carbon monoxide poisoning caused by a gas leak in her home. One result of her brain damage was that D.F. was not able to match the orientation of a card held in her hand to different orientations of a slot. This is shown in the left circle in **Figure 4.26a**, which indicates D.F.'s attempts to match the orientation of a vertical slot. Perfect matching performance would be indicated by a vertical line for each trial, but D.F.'s responses are widely scattered across many different orientations. The right circle shows the accurate performance of the normal controls.

Because D.F. had trouble orienting a card to match the orientation of the slot, it would seem reasonable that she would also have trouble *placing* the card through the slot, because to do this she would have to turn the card so that it was lined up with the slot. But when D.F. was asked to "mail" the card through the slot, she could do it! Even though D.F. could not turn the card to visually match the slot's orientation, once she started moving the card toward the slot, she was able to rotate it to match the orientation of the slot (**Figure 4.26b**). Thus, D.F. performed poorly in the *static orientation-matching task* but did well as soon as *action* was involved (Murphy et al., 1996). Milner and Goodale interpreted D.F.'s behavior as showing that there is one mechanism for judging orientation and another for coordinating vision and action (Goodale, 2014).

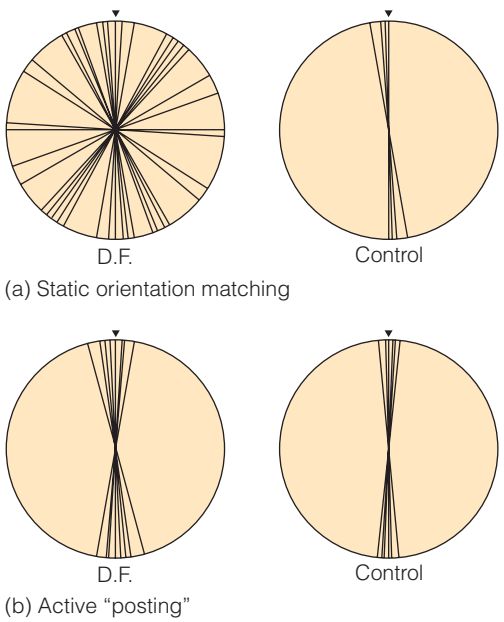

Figure 4.26 Performance of patient D.F. and a person without brain damage on two tasks: (a) judging the orientation of a slot and (b) placing a card through the slot. Vertical lines indicate perfect matching performance. (Milner & Goodale, 1995)

These results for D.F. are part of a double dissociation because there are other patients whose symptoms are the opposite of D.F.'s. These people can judge visual orientation, but they can't accomplish the task that combines vision and action. As we would expect, whereas D.F.'s ventral stream is damaged, these other people have damage to their dorsal streams.

Based on these results, Milner and Goodale suggested that the ventral pathway should still be called the *what* pathway, as Ungerleider and Mishkin suggested, but that a better description of the dorsal pathway would be the ***how* pathway**, or the ***action* pathway**, because it determines *how* a person carries out an *action*. As sometimes occurs in science, not everyone uses the same terms. Thus, some researchers call the dorsal stream the *where* pathway, and some call it the *how* or *action* pathway.

The Behavior of People Without Brain Damage

In our normal daily behavior, we aren't aware of two visual processing streams, one for *what* and the other for *how*, because they work together seamlessly as we perceive objects and take actions toward them. Cases like that of D.F., in which one stream is damaged, reveal the existence of these two streams. But what about people without damaged brains? Psychophysical experiments that measure how people perceive and react to visual illusions have demonstrated the dissociation between perception and action that was evident for D.F.

Figure 4.27a shows the stimulus used by Tzvi Ganel and coworkers (2008) in an experiment designed to demonstrate a separation of perception and action in non-brain-damaged participants. This stimulus creates a visual illusion: Line 1 is actually longer than line 2 (see **Figure 4.27b**), but line 2 *appears* longer.

Ganel and coworkers presented participants with two tasks: (1) a *length estimation task* in which they were asked to indicate how they perceived the lines' length by spreading their thumb and index finger, as shown in **Figure 4.27c**; and (2) a *grasping task* in which they were asked to reach toward the lines and grasp each line by its ends. Sensors on the participants' fingers measured the separation between the fingers as the participants grasped the lines. These two tasks were chosen because they depend on different processing streams. The length estimation task involves the ventral or *what* stream. The grasping task involves the dorsal or *where/how* stream.

The results of this experiment, shown in **Figure 4.27d**, indicate that in the length estimation task, participants judged line 1 (the longer line) as looking shorter than line 2, but in the grasping task, they separated their fingers farther apart for line 1 to match its longer length. Thus, the illusion works for perception (the length estimation task), but not for action (the grasping task). These results support the idea that perception and action are served by different mechanisms. An idea about functional organization that originated with observations of

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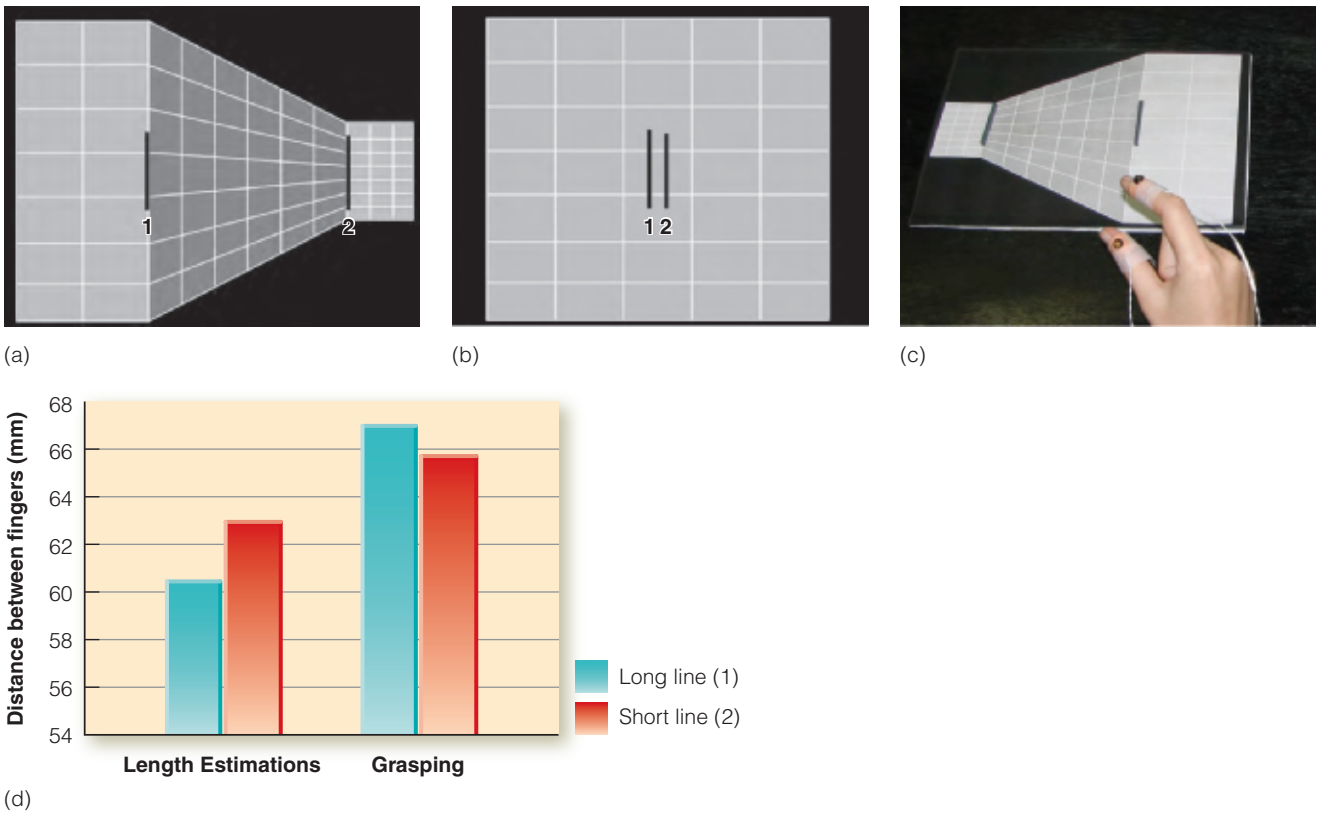

Figure 4.27 (a) The size illusion used by Ganel and coworkers (2008) in which line 2 looks longer than line 1. The numbers were not present in the display seen by the participants. (b) The two vertical lines from (a), showing that line 2 is actually shorter than line 1. (c) Participants in the experiment adjusted the space between their fingers either to estimate the length of the lines (length estimation task) or to reach toward the lines to grasp them (grasping task). The distance between the fingers is measured by sensors on the fingers. (d) Results of the length estimation and grasping tasks in the Ganel et al. experiment. The length estimation task indicates the illusion, because the shorter line (line 2) was judged to be longer. In the grasping task, participants separated their fingers more for the longer line (line 1), which was consistent with the physical lengths of the lines. (From Ganel et al., 2008)

patients with brain damage is therefore supported by the performance of participants without brain damage.

4.5 Higher-Level Neurons

At this point in the chapter, we have seen how the visual signal travels from the retina to the visual cortex, then on to extrastriate areas, and the *what* and *where/how* processing streams (keeping in mind that signals flow both "up" and "down" these pathways). Now we'll discuss how information is represented at higher levels of the visual system by considering the responses of individual neurons within these areas.

Responses of Neurons in Inferotemporal Cortex

We focused on the firing of individual neurons in this chapter when we discussed the feature detectors in the visual cortex and how they respond to basic elements of a visual scene. Now, let's again consider neural responses, but at a higher level—in the temporal lobe.

An area in the temporal lobe that has been the focus of much research is the **inferotemporal (IT) cortex** (Figure 4.23). Recall that earlier in this chapter, we mentioned how receptive fields of neurons in the visual system become larger as we move to higher levels, like from striate to extrastriate cortex. As it turns out, this increase in receptive field size continues through the *what* stream so that neurons at the apex of this stream in IT cortex have the largest receptive fields—large enough to encompass whole objects in one's visual field. So, it would make sense that instead of responding to simple features like lines or edges, like V1 neurons, IT neurons would respond to more complex objects that occupy a larger portion of the visual field.

This knowledge comes from early experiments conducted by Charles Gross and coworkers (1972), who recorded from single neurons in the monkey's IT cortex. In these experiments, Gross's research team presented a variety of stimuli to anesthetized monkeys. Using the projection screen procedure, they presented lines, squares, and circles. Some stimuli were light,

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and some dark. The dark stimuli were created by placing cardboard cutouts against the transparent projection screen.

The discovery that neurons in the IT cortex respond to complex stimuli came a few days into one of their experiments, when they found a neuron that refused to respond to any of the standard stimuli like oriented lines or circles or squares. Nothing worked, until one of the experimenters pointed at something in the room, casting a shadow of his hand on the screen. When this hand shadow caused a burst of firing, the experimenters knew they were on to something and began testing the neuron to see what kinds of stimuli caused it to respond. They used a variety of stimuli, including cutouts of a monkey's hand. After a great deal of testing, they determined that this neuron responded to a handlike shape with fingers pointing up (**Figure 4.28**) (Rocha-Miranda, 2011; also see Gross, 2002, 2008). After expanding the types of stimuli presented, they also found some neurons that responded best to faces.

Finding neurons that responded to real-life, complex objects like hands and faces was a revolutionary result. Apparently, neural processing that occurred beyond the initial receiving areas studied by Hubel and Wiesel had created neurons that responded best to very specific types of stimuli. But sometimes revolutionary results aren't accepted immediately, and Gross's results were largely ignored when they were published in 1969 and 1972 (Gross et al., 1969, 1972). Finally, in the 1980s, other experimenters began recording from neurons in the IT cortex of the monkey that responded to faces and other complex objects (Perrett et al., 1982; Rolls, 1981).

In 1995, Edmund Rolls and Martin Tovee found many neurons in the IT cortex in monkeys that responded best to faces, further confirming Gross's initial findings that IT neurons respond to specific types of complex stimuli. **Figure 4.29** shows the results for a neuron that responded to faces but hardly at all to other types of stimuli. What is particularly significant about such "face neurons" is that, as it turns out, there are areas in the monkey temporal lobe that are particularly rich in these neurons. Doris Tsao and coworkers (2006) presented 96 images of faces, bodies, fruits, gadgets, hands, and scrambled patterns to two monkeys while recording from cortical neurons inside this "face area." They classified neurons as "face selective" if they responded at least twice as strongly to faces as to nonfaces. Using this criterion, they found that 97 percent of the cells were face selective. The high level of face selectivity within this area is illustrated in **Figure 4.30**, which shows the average response for both monkeys to each of the 96 objects. The response to the 16 faces, on the left, is far greater than the response to any of the other objects.

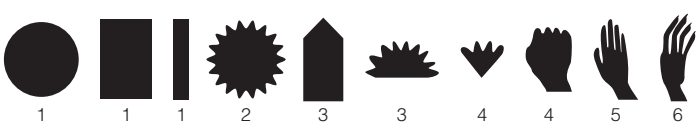

Figure 4.28 Some of the shapes used by Gross and coworkers (1972) to study the responses of neurons in the monkey's inferotemporal cortex. The shapes are arranged in order of their ability to cause the neuron to fire, from none (1) to little (2 and 3) to maximum (6). (From Gross et al., 1972)

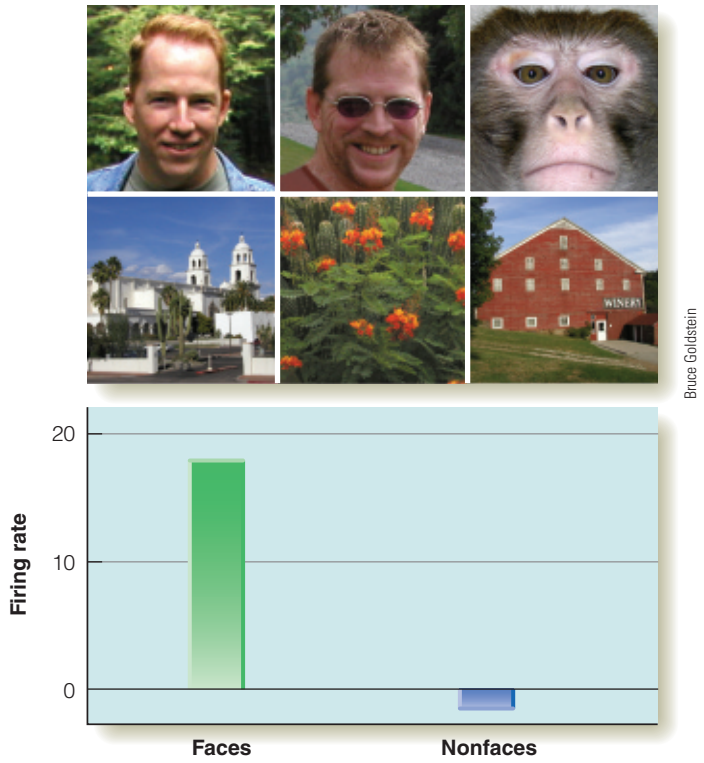

Figure 4.29 Size of response of a neuron in the monkey's IT cortex that responds to face stimuli but not to nonface stimuli. (Based on data from Rolls & Tovee, 1995)

Clearly, Charles Gross was onto something with his discovery of IT neuron specificity—an idea which was later supported by these studies finding face-selective neurons grouped together in IT cortex. As it turns out, evidence for face selectivity has been observed in the human brain as well (Kanwisher et al., 1997; McCarthy et al., 1997). We'll discuss how the human brain responds to faces and other complex objects in the next chapter.

We can take this idea of neural activity for complex objects a step further by considering that the processes we have been describing not only create perceptions, but they also provide information that is stored in our memory so we can remember perceptual

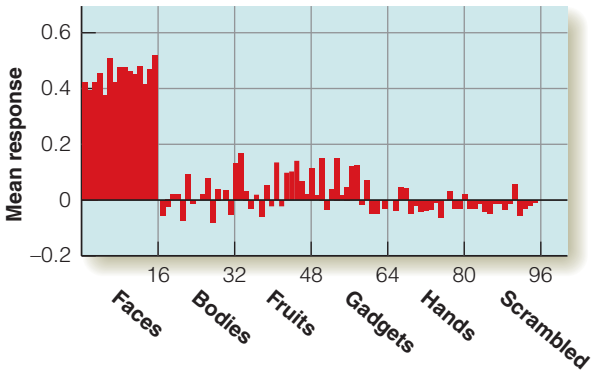

Figure 4.30 Results of the Tsao et al. (2006) experiment in which activity of neurons in the monkey's temporal lobe was recorded in response to faces, other objects, and a scrambled stimulus. (From Tsao et al., 2006)

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experiences later. This link between perception and memory has been studied in a number of experiments that have measured responding in single neurons in the human hippocampus, an area associated with forming and storing memories.

Where Perception Meets Memory

Some of the signals leaving the IT cortex reach structures in the medial temporal lobe (MTL), such as the parahippocampal cortex, the entorhinal cortex, and the hippocampus (**Figure 4.31**). These MTL structures are extremely important for memory. The classic demonstration of the importance of one of the structures in the MTL, the hippocampus, is the case of H.M., who had his hippocampus on both sides of his brain removed in an attempt to eliminate epileptic seizures that had not responded to other treatments (Scoville & Milner, 1957).

The operation eliminated H.M.'s seizures, but it also eliminated his ability to store experiences in his memory. Thus, when H.M. experienced something, such as a visit from his doctor, he was unable to remember the experience, so the next time the doctor appeared, H.M. had no memory of having seen him. H.M.'s unfortunate situation occurred because in 1953, the surgeons did not realize that the hippocampus is crucial for the formation of long-term memories. Once they realized the devastating effects of removing the hippocampus on both sides of the brain, H.M.'s operation was never repeated.

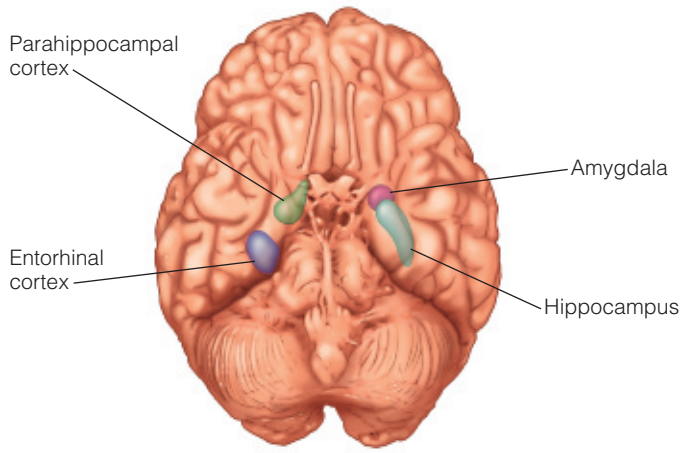

Figure 4.31 Location of the hippocampus, entorhinal cortex, parahippocampal cortex, and amygdala on the underside of the brain.

We saw evidence of the link between the hippocampus and vision in Chapter 2 when we discussed specificity coding and the research by Quiroga and coworkers (2005, 2008). Recall that these studies showed that there are neurons in the hippocampus that respond to specific stimuli, like the Sydney Opera House or Steve Carell (see Figure 2.11, page 28). As it turns out, these hippocampal and MTL neurons respond not only to the visual perception of specific objects or concepts, but also the *memories* of those concepts.

Evidence of this link between MTL neurons that respond to visual stimuli and memories comes from an experiment by Hagan Gelbard-Sagiv and coworkers (2008). These researchers had epilepsy patients view a series of 5- to 10-second video clips a number of times while recording from neurons in the MTL. The clips showed famous people, landmarks, and nonfamous people and animals engaged in various actions. As the person was viewing the clips, some neurons responded better to certain clips. For example, a neuron in one of the patients responded best to a clip from *The Simpsons* TV program.

The firing to specific video clips is similar to what Quiroga found for viewing still pictures. However, this experiment went a step further by asking the patients to think back to any of the film clips they had seen while the experimenter continued to record from the MTL neurons. One result is shown in **Figure 4.32**, which indicates the response of the neuron that fired to *The Simpsons*. The patient's description of what he was remembering is shown at the bottom of the figure. First the patient remembered "something about New York," then "the Hollywood sign." The neuron responds weakly or not at all to those two memories. However, remembering *The Simpsons* causes a large response, which continues as the person continues remembering the episode (indicated by the laughter). Results such as this support the idea that the neurons in the MTL that respond to *perceiving* specific objects or events may also be involved in *remembering* these objects and events. (Also see Cerf and coworkers [2010] for more on how thoughts can influence the firing of higher-level neurons.)

Throughout this chapter, we have seen how individual neurons at various stages respond to visual input, and even memories of that visual input. We will continue to discuss more specific aspects of vision in upcoming chapters, including the functions of other brain areas within the processing streams we've introduced here.

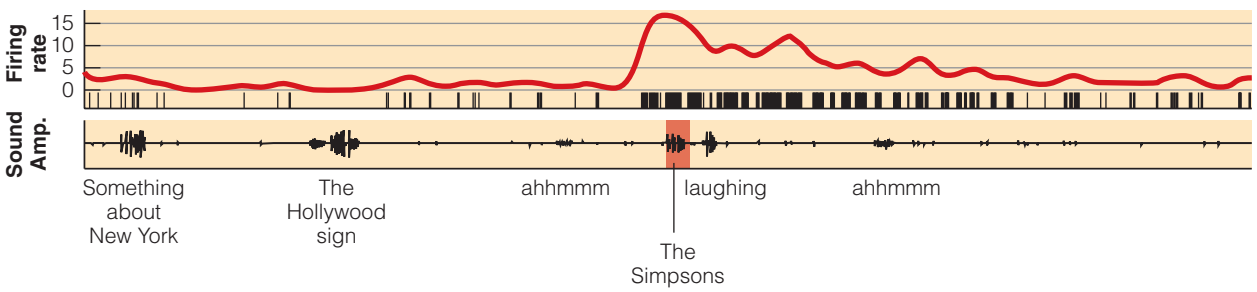

Figure 4.32 Activity of a neuron in the MTL of an epilepsy patient remembering the things indicated below the record. A response occurs when the person remembered *The Simpsons* TV program. Earlier, this neuron had been shown to respond to viewing a video clip of *The Simpsons*. (From Gelbard-Sagiv et al., 2008)

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SOMETHING TO CONSIDER:

"Flexible" Receptive Fields

In Chapter 3, we introduced the idea of a neuron's receptive field by defining the receptive field as *the area of the retina that, when stimulated, influences the firing of the neuron*. Later, as we worked our way to higher levels of the visual system, the receptive field was still the area that affected firing, but the stimulus required became more specific—oriented lines, geometrical shapes, and faces.

Nowhere in our discussion of receptive fields did we say that the area defining the receptive field can change. Receptive fields are, according to what we have described so far, static, wired-in properties of neurons. However, one of the themes of this book—and of a great deal of research in perception—is that because we exist in an ever-changing environment, because we are often moving, experiencing new situations, and creating our own goals and expectations, we need a perceptual system that is flexible and adapts to our needs and to the current situation. This section—in which we introduce the idea that the visual system is flexible and that neurons can change depending on changing conditions—is a "preview of coming events," because the idea that sensory systems are flexible will recur throughout the book.

An example of how a neuron's response can be affected by what is happening outside the neuron's receptive field is illustrated by the results of an experiment by Mitesh Kapadia and coworkers (2000), in which they recorded from neurons in a monkey's visual cortex. **Figure 4.33a** indicates the response of a neuron to a vertical bar located inside the neuron's receptive field, which is indicated by the bar inside the square. **Figure 4.33b** shows that two vertical bars located outside the neuron's receptive field cause little change in the neuron's response. But **Figure 4.33c** shows what happens when the "outside the receptive field" bars are presented along with the "inside the field" bar. There is a large increase in firing! Thus, although our definition of a neuron's receptive field as *the area of retina which, when stimulated, influences the neuron's firing*, is still correct, we can now see that the response to stimulation *within* the receptive field can be affected by what's happening *outside* the receptive field.

The effect of stimulating outside the receptive field is called **contextual modulation**. The large response that occurs when the three lines are presented together may be related to an example of a perceptual phenomenon called *perceptual organization*, illustrated in **Figure 4.33d**, which shows how lines of the same orientation are perceived as a group that stands out from the surrounding clutter. We will consider perceptual organization further in Chapter 5, "Perceiving Objects and Scenes."

In Chapter 6, "Visual Attention," we will consider the many effects of paying attention. When we pay attention to something, we become more aware of it, we can respond more rapidly to it, and we may even perceive it differently. And as we will see, attention can even shift the location of a neuron's receptive field (Figure 6.23). This shifting of the receptive field is an amazing result because it means that attention is changing the organization of part of the visual system. Receptive fields, it turns out, aren't fixed in place but can change in response to where someone is paying attention. This concentrates neural processing power at the place that is important to the person at that moment. As we continue exploring how the nervous system creates our perceptions, we will encounter other examples of how the flexibility of our nervous system helps us function within our ever-changing environment.

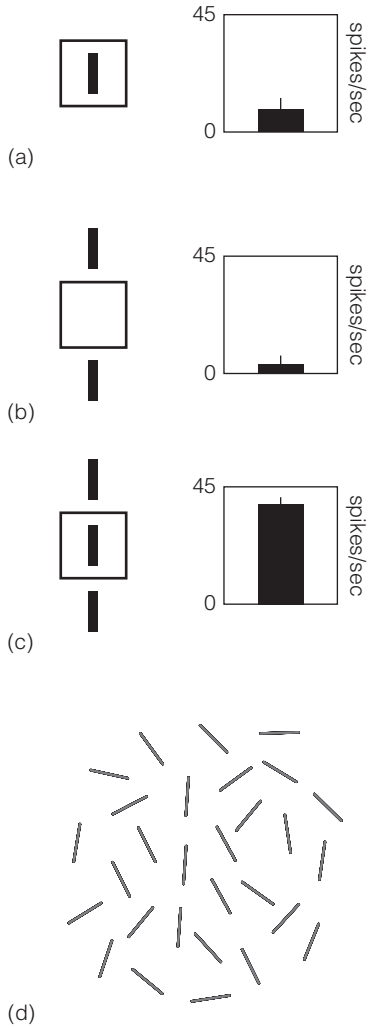

Figure 4.33 A neuron in the monkey's temporal lobe responds (a) with a small response to a vertical bar flashed inside the receptive field (indicated by the square); (b) with little or no response to two vertical bars presented outside the receptive field; (c) with a large response when the three bars are presented together. This enhanced response caused by stimuli presented outside the receptive field is called *contextual modulation*. (d) A pattern in which the three aligned lines stand out. (a–c from Kapadia et al., 2000)

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TEST YOURSELF 4.2

1. What is the extrastriate cortex? How do receptive fields of extrastriate neurons differ from receptive fields of striate neurons?
2. How has ablation been used to demonstrate the existence of the ventral and dorsal processing streams? What is the function of these streams?
3. How has double dissociation been used to show that one of the functions of the dorsal stream is to process information about coordinating vision and action? How do the results of a behavioral experiment support the idea of two primary streams in people without brain damage?
4. Describe Gross's experiments on neurons in the inferotemporal cortex of the monkey. Why do you think his results were initially ignored?
5. Describe the connection between vision and memory, as illustrated by experiments that recorded from neurons in the MTL and hippocampus.
6. Describe the two experiments that demonstrated the "flexibility" of receptive fields.

THINK ABOUT IT

1. Ralph is hiking along a trail in the woods. The trail is bumpy in places, and Ralph has to avoid tripping on occasional rocks, tree roots, or ruts in the trail. Nonetheless, he is able to walk along the trail without constantly looking down to see exactly where he is placing his feet. That's a good thing because Ralph enjoys looking out at the woods to see whether he can spot interesting birds or animals. How can you relate this description of Ralph's behavior to the operation of the dorsal and ventral streams in the visual system? (p. 80)
2. Cell A responds best to vertical lines moving to the right. Cell B responds best to 45-degree lines moving to the right. Both of these cells have an excitatory synapse with cell C. How will cell C fire to vertical lines? To 45-degree lines? What if the synapse between B and C is inhibitory?
3. We have seen that the neural firing associated with an object in the environment does not necessarily look like, or resemble, the object. Can you think of situations that you encounter in everyday life in which objects or ideas are represented by things that do not exactly resemble those objects or ideas?

KEY TERMS

Ablation (p. 80)
Action pathway (p. 82)
Area V1 (p. 69)
Complex cells (p. 70)
Contextual modulation (p. 86)
Contralateral (p. 68)
Contrast threshold (p. 72)
Cortical magnification (p. 75)
Cortical magnification factor (p. 75)
Dorsal pathway (p. 81)
Double dissociations (p. 81)
End-stopped cell (p. 71)
Experience-dependent plasticity (p. 74)
Extrastriate cortex (p. 79)
Feature detectors (p. 71)
Hippocampus (p. 85)
How pathway (p. 82)
Hypercolumn (p. 78)
Inferotemporal (IT) cortex (p. 83)
Landmark discrimination problem (p. 80)
Lateral geniculate nucleus (LGN) (p. 68)
Location columns (p. 77)
Neural plasticity (p. 74)
Object discrimination problem (p. 80)
Optic chiasm (p. 68)
Orientation columns (p. 77)
Orientation tuning curve (p. 70)
Retinotopic map (p. 75)
Selective adaptation (p. 72)
Selective rearing (p. 74)
Simple cortical cell (p. 70)
Striate cortex (p. 69)
Superior colliculus (p. 68)
Tiling (p. 79)
Ventral pathway (p. 81)
Visual receiving area (p. 69)
What pathway (p. 80)
Where pathway (p. 81)

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Wherever you look, whether it's walking across campus, sitting in your room, or looking at this hillside town of Manarola, Italy, you perceive small details, individual objects, and larger scenes created from these objects. Although you usually achieve these perceptions with ease, they are created by extremely complex, hidden, processes.

Bruce Goldstein

Learning Objectives

After studying this chapter, you will be able to …

- Discuss why object perception is challenging for both humans and computers.
- Explain Gestalt psychology and the laws of perceptual organization.
- Define figure–ground segregation and identify the properties that determine which area is perceived as figure.
- Describe the recognition by components theory and how it accounts for our ability to recognize objects from different viewpoints.
- Explain the role of past experience, inference, and prediction in perception.
- Describe experiments that show how the brain responds to faces, bodies, and scenes, and what is meant by "neural mind reading."
- Analyze the evidence for and against the idea that faces are "special."
- Discuss the development of face recognition in infants.

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CHAPTER 5

Perceiving Objects and Scenes

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TEST YOURSELF 5.2

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TEST YOURSELF 5.3

THINK ABOUT IT

Some Questions We Will Consider:

- Why are even the most sophisticated computers unable to match a person's ability to perceive objects? (p. 91)
- Why do some perceptual psychologists say "The whole differs from the sum of its parts"? (p. 96)
- Can we tell what people are perceiving by monitoring their brain activity? (p. 110)
- Are faces special compared to other objects like cars or houses? (p. 116)
- How do infants perceive faces? (p. 118)

Sitting in the upper deck in PNC Park, home of the Pittsburgh Pirates, Roger looks out over the city (**Figure 5.1**). He sees a group of about 10 buildings on the left and can easily tell one building from another. Looking straight ahead, he sees a small building in front of a larger one, and has no trouble telling that they are two separate buildings. Looking down toward the river, he notices a horizontal yellow band above the right field bleachers. It is obvious to him that this is not part of the ballpark but is located across the river.

All of Roger's perceptions come naturally to him and require little effort. But when we look closely at the scene, it becomes apparent that the scene poses many "puzzles." The following demonstration points out a few of them.

DEMONSTRATION | Perceptual Puzzles in a Scene

The questions below refer to the areas labeled in Figure 5.1. Your task is to answer each question and indicate the reasoning behind each answer:

What is the dark area at A?

Are the surfaces at B and C facing in the same or different directions?

Are areas B and C on the same or on different buildings?

Does the building at D extend behind the one at A?

Although it may have been easy to answer the questions, it was probably somewhat more challenging to indicate what

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Bruce Goldstein

Figure 5.1 It is easy to tell that there are a number of different buildings on the left and that straight ahead there is a low rectangular building in front of a taller building. It is also possible to tell that the horizontal yellow band above the bleachers is across the river. These perceptions are easy for humans but would be quite difficult for a computer vision system. The letters on the left indicate areas referred to in the Demonstration on page 89.

your "reasoning" was. For example, how did you know the dark area at A is a shadow? It could be a dark-colored building that is in front of a light-colored building. Or on what basis might you have decided that building D extends behind building A? It could, after all, simply end right where A begins. We could ask similar questions about everything in this scene because, as we will see, a particular pattern of shapes can be created by a large number of objects.

One of the messages of this chapter is that we need to go beyond the pattern of illumination that a scene creates on the retina to determine what is "out there." One way to appreciate the importance of this "going beyond" process is to consider how difficult it has been to program even the most powerful computers to accomplish perceptual tasks that humans achieve with ease.

We saw an example of computer errors in Chapter 1 (p. 4) when we discussed a recent study showing how computers, when learning how to identify objects in a scene, sometimes make errors that humans wouldn't make, like mistaking a toothbrush for a baseball bat (see Figure 1.2). In that study, the computer was programmed to generate descriptions of a scene based on the objects that it detected in the image (Karpathy & Fei-Fei, 2015). To create the description, "a young boy is holding a baseball bat" the computer first had to detect the objects in the image and then match those objects to existing, stored representations of what those objects are—a process known as **object recognition**. In this case, the computer recognized the objects as (1) a boy and (2) a baseball bat, and then created a description of the scene.

Other computer vision systems have been designed to learn how to recognize objects and determine not a description of a scene, but rather, the precise locations of objects in that scene. **Figure 5.2** shows how computers can do this by placing boxes around the recognized objects (Redmon et al., 2016, 2018). This object recognition and localization can occur, with little delay, in real-time (Boyla et al., 2019).

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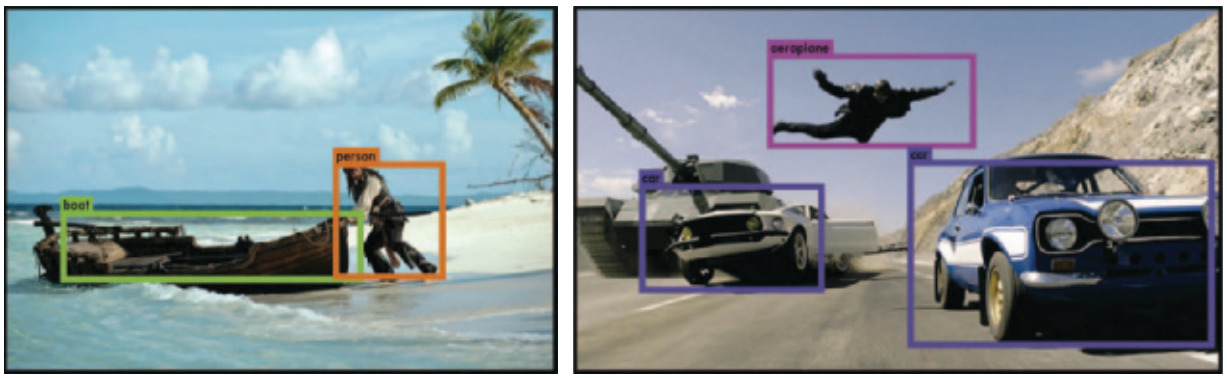

(a) (b)

Figure 5.2 Examples of output from a computer system designed to detect and recognize objects in images. The labels and boxes in these images were created by the computer program. (a) The computer correctly identified the boat and the person. (b) The computer correctly identified the cars but calls the person an "aeroplane." (From Redmon et al., 2016)

This type of technology is what underlies developments like autonomous vehicles, which require fast and precise identification of objects in order to smoothly navigate the environment. Think of all the objects that such a vehicle must quickly and accurately detect and recognize while driving down the road—pedestrians, cyclists, potholes, and curbs, as well as road markings like lane dividers. This technology is extremely impressive, and is probably in your pocket, as cellphones rely on object recognition all the time, whether it be learning to recognize your face across different angles and lighting conditions in order to unlock your device, or an app that identifies a specific type of plant in a picture that you took.

The field of computer vision has clearly come a long way, especially in the past 10 or so years. Just from 2012 to 2017, average error rates of these computer vision systems dropped from 16 percent to a mere 2 percent (Liu et al., 2019), meaning that they were wrong only 2 percent of the time—a number that is likely to have dropped even lower from the time this book was written to when you are reading it. Computers are becoming so accurate, in fact, that in some situations, their object detection performance sometimes matches or even exceeds that of humans (Geirhos et al., 2018). An exciting (and perhaps scary) prospect!

And yet, even with all of these advancements, these computer systems still fail to fully replicate the intricacies of human vision. Where they often fall short is in identifying objects under degraded conditions—like when an image is blurry—or in uncommon or unexpected situations. An example of one such error arising from an uncommon situation is shown in the image of the car chase in the bottom row of Figure 5.2b (Redmon et al., 2016). We as humans can clearly identify the object in the air as a person leaping from car to car, but since it's not common for a person to be flying through the air, and also due to the shape of the image, the computer program misidentified that object as an airplane.

What's interesting is that while object and scene perception is difficult for computers, it is easy for humans—so easy, in fact, that we often don't even have to think about it ("Of course that's a person leaping through the air and not an airplane!"). This is yet another example of how, although we're getting closer, we haven't yet created a "perceiving machine" that accounts for all of the complexities of human perception.

5.1 Why Is It So Difficult to Design a Perceiving Machine?

We will now describe a few of the problems involved in designing a "perceiving machine." Remember that the point of these problems is that although they pose difficulties for computers, humans solve them easily.

The Stimulus on the Receptors Is Ambiguous

When you look at a page of a book, the image cast by the borders of the page on your retina is ambiguous. It may seem strange to say that, because (1) the rectangular shape of the page is obvious, and (2) once we know the page's shape and its distance from the eye, determining its image on the retina is a simple geometry problem, which, as shown in **Figure 5.3**, can be solved by extending "rays" from the red corners of the page into the eye.

But the perceptual system is not concerned with determining an object's image on the retina. It *starts* with the image on the retina, and its job is to determine the object "out there" that *created* the image. The task of determining the object

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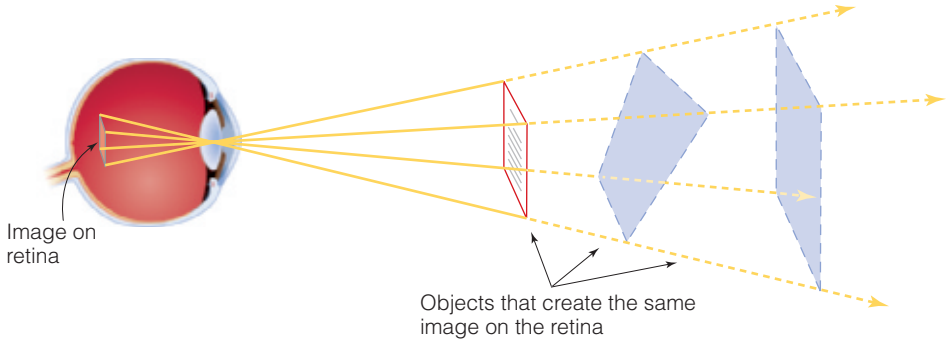

Figure 5.3 The projection of the book (red object) onto the retina can be determined by extending rays (solid lines) from the corners of the book into the eye. The principle behind the inverse projection problem is illustrated by extending rays out from the eye past the book (dashed lines). When we do this, we can see that the image created by the book can be created by an infinite number of objects, among them the tilted trapezoid and the large rectangle shown here. This is why we say that the image on the retina is ambiguous.

responsible for a particular image on the retina is called the **inverse projection problem**, because it involves starting with the retinal image and extending rays *out* from the eye. When we do this, as shown by extending the lines in Figure 5.3, we see that the retinal image created by the rectangular page could have been created by a number of other objects, including a tilted trapezoid, a much larger rectangle, and an infinite number of other objects located at different distances. When we consider that the flat two-dimensional image on the retina can be created by many different objects in the environment, it is easy to see why we say that the image on the retina is ambiguous.

Artists have taken advantage of the fact that two-dimensional projections, like the image on the retina, can be created by many different objects, to create interesting "art constructions." Consider, for example, **Figure 5.4**, which shows an art installation by Shigeo Fukuda, in which a spotlight shining on a stack of bottles and glassware casts a two-dimensional shadow on the wall that looks like a silhouette of a woman with an umbrella. This shadow is a two-dimensional projection of the stack of bottles that occurs when the light casting the shadow is placed in just the right location. Similarly, it is possible that the two-dimensional image on the retina may not accurately reflect what is "out there" in the environment.

The ambiguity of the image on the retina is also illustrated by **Figure 5.5a**, which, when viewed from one specific location, creates a circular image on the retina and appears to be a circle of rocks. However, moving to another viewpoint

Estate of Shigeo Fukuda

Figure 5.4 "Bonjour Madamoiselle" art piece by Shigeo Fukuda, showing how the image projected onto a surface (the shadow on the wall that looks like a woman) doesn't always accurately depict what is out there in the environment (a precarious stack of bottles and glassware).

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Thomas Macaulay

(a) (b)

Figure 5.5 An environmental sculpture by Thomas Macaulay. (a) When viewed from the exact right vantage point (the second-floor balcony of the Blackhawk Mountain School of Art, Black Hawk, Colorado), the stones appear to be arranged in a circle. (b) Viewing the stones from the ground floor reveals a truer indication of their configuration. (Courtesy of Thomas Macaulay, Blackhawk Mountain School of Art, Blackhawk, CO)

reveals that the rocks aren't arranged in a circle after all (**Figure 5.5b**). Thus, just as a rectangular image on the retina can be created by trapezoids and other nonrectangular objects, a circular image on the retina can be created by objects that aren't circular.

The art pieces depicted in Figures 5.4 and 5.5 are designed to fool us by relying on viewing conditions that create images that don't correspond to the actual object. Most of the time, erroneous perceptions like this don't occur; the visual system solves the inverse projection problem and determines which object out of all the possible objects is responsible for a particular image on the retina. However, as easy as this is for the human perceptual system, solving the inverse projection problem poses serious challenges to computer vision systems.

Objects Can Be Hidden or Blurred

Sometimes objects are hidden or blurred. For example, look for the pencil and eyeglasses in **Figure 5.6** before reading further. Although it might take a little searching, people can find the pencil in the foreground and the glasses frame sticking out from behind the computer, next to the picture, even though only a small portion of these objects is visible. People can also easily identify the book, scissors, and paper, even though they are partially hidden by other objects.

This problem of hidden objects occurs anytime one object obscures—or "occludes"—part of another object. This occurs frequently in the environment, but people easily understand that the part of an object that is covered continues to exist,

Bruce Goldstein

Figure 5.6 A portion of the mess on the author's desk. Can you locate the hidden pencil (easy) and the author's glasses (hard)?

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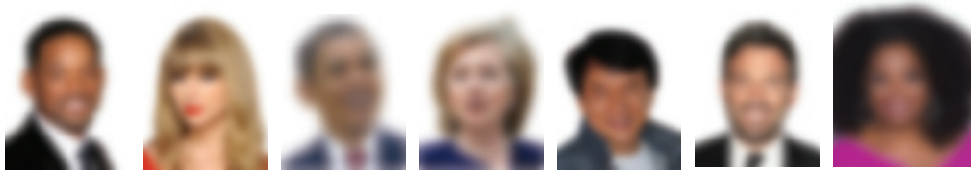

Figure 5.7 Who are these people? See page 120 for the answers. (bukley/ Shutterstock.com; Featureflash/Shutterstock.com; dpa picture alliance archive/Alamy Stock Photo; Peter Muhly/Alamy Stock Photo; s_bukley/ Shutterstock.com; Joe Seer/Shutterstock.com; DFree/Shutterstock.com)

and they are able to use their knowledge of the environment to determine what is likely to be present.

People are also able to recognize objects that are not in sharp focus, such as the faces in **Figure 5.7**. See how many of these people you can identify, and then consult the answers on page 120. Despite the degraded nature of these images, people can often identify most of them, whereas computers still perform poorly on this type of task (Li et al., 2018).

Objects Look Different From Different Viewpoints

Another problem facing any perceiving machine is that objects are often viewed from different angles. This means that the images of objects are continually changing, depending on the angle from which they are viewed. Thus, although humans continue to perceive the object in **Figure 5.8** as the same chair viewed from different angles, this isn't so obvious to a computer. The ability to recognize an object seen from different viewpoints is called viewpoint invariance—a task that is difficult for computers.

The difficulties facing any perceiving machine illustrate that the process of perception is more complex than it seems (something you already knew from the perceptual process in Figure 1.1, page 4). But how do humans overcome these complexities? We begin answering this question by considering *perceptual organization*.

5.2 Perceptual Organization

Perceptual organization is the process by which elements in a person's visual field become perceptually grouped and segregated to create a perception. During this process, incoming stimulation is organized into coherent units such as objects. The process of perceptual organization involves two components: *grouping* and *segregation* (**Figure 5.9**; Peterson & Kimchi, 2013). Grouping is the process by which elements in a visual scene are "put together" into coherent units or objects. Thus, when Roger sees each building in Pittsburgh as an individual unit, he has grouped the visual elements in the scene to create each building. If you can perceive the Dalmatian dog in **Figure 5.10**, you have perceptually grouped some of the dark areas to form a Dalmatian, with the other dark areas being seen as shadows on the ground.

The process of grouping works in conjunction with segregation, which is the process of separating one area or object from another. Thus, seeing two buildings in Figure 5.9 as separate from one another, with borders indicating where one building ends and the other begins, involves segregation.

The Gestalt Approach to Perceptual Grouping

What causes some elements to become grouped so they are part of one object? Answers to this question were provided in the early 1900s by the Gestalt psychologists—where *Gestalt*, roughly translated, means *configuration*. "How," asked the Gestalt psychologists, "are configurations formed from smaller elements?"

We can understand the Gestalt approach by first considering an approach that came before Gestalt psychology, called *structuralism*, which was proposed by Wilhelm Wundt, who established the first laboratory of scientific psychology at the University of Leipzig in 1879. Structuralism distinguished between *sensations*—elementary processes that occur in response to stimulation of the senses—and *perceptions*, more complex conscious experiences such as our awareness of objects. The structuralists saw sensations as analogous to the atoms of

(a) (b) (c)

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Figure 5.8 Your ability to recognize each of these views as being of the same chair is an example of viewpoint invariance.

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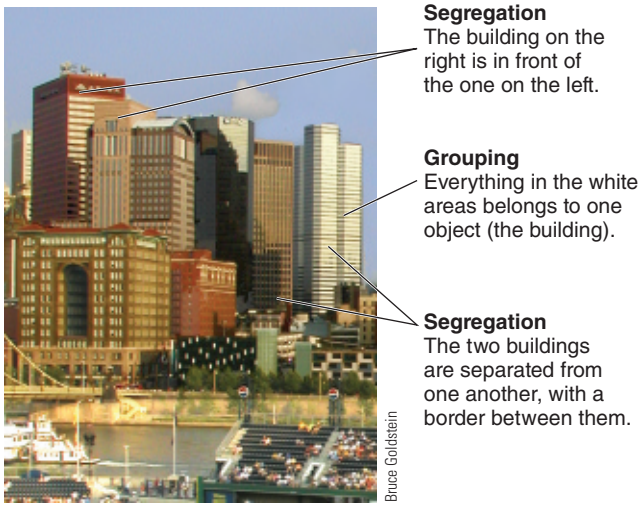
Segregation
The building on the right is in front of the one on the left.
Grouping
Everything in the white areas belongs to one object (the building).
Segregation
The two buildings are separated from one another, with a border between them.
Bruce Goldstein

Figure 5.9 Examples of grouping and segregation in a city scene.

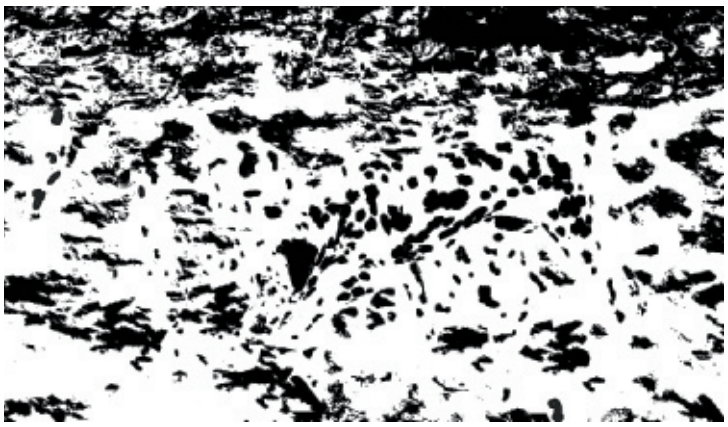

Figure 5.10 Some black and white shapes that become perceptually organized into a Dalmatian. See page 120 for an outline of the Dalmatian.

chemistry. Just as atoms combine to create complex molecular structures, sensations combine to create complex perceptions. Sensations might be linked to very simple experiences, such as seeing a single flash of light, but perception accounts for the vast majority of our sensory experiences. For example, when you look at **Figure 5.11**, you perceive a face, but according to structuralists, the starting point would be many sensations, which are indicated by the small dots.

The Gestalt psychologists rejected the idea that perceptions were formed only by "adding up" sensations. An early observation that led to rejecting the idea of adding up sensations occurred in 1911, as psychologist Max Wertheimer was on vacation taking a train ride through Germany (Boring, 1942). When Wertheimer got off the train to stretch his legs in Frankfort, he made an observation that involved a phenomenon called *apparent movement*.

Apparent Movement On the train platform in Frankfort, Wertheimer bought a toy stroboscope from a vendor. The stroboscope, which is a mechanical device that creates an illusion of movement by rapidly alternating two slightly different pictures, caused Wertheimer to wonder how the structuralist's idea that experience is created by sensations could explain the illusion of movement he observed.

Figure 5.12 diagrams the principle behind the illusion of movement created by the stroboscope, which is called **apparent movement** because although movement is perceived, nothing is actually moving. The three components that create apparent movement (in this case, using flashing lights) are shown in Figure 5.12: (a) One light flashes (**Figure 5.12a**); (b) there is a

Figure 5.11 According to structuralism, a number of sensations (represented by the dots) add up to create our perception of the face.

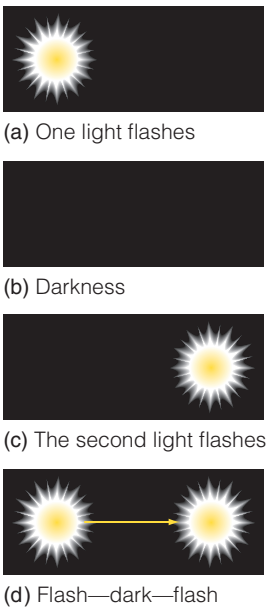

Figure 5.12 The conditions for creating apparent movement. (a) One light flashes, followed by (b) a short period of darkness, followed by (c) another light flashing in a different position. The resulting perception, symbolized in (d), is a light moving from left to right. Movement is seen between the two lights even though there is only darkness in the space between them.

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period of darkness, lasting a fraction of a second (**Figure 5.12b**); and (c) the second image flashes (**Figure 5.12c**). Physically, then, there are two images flashing separated by a period of darkness. But we don't see the darkness because our perceptual system adds something during the period of darkness—the perception of an image moving through the space between the flashing lights (**Figure 5.12d**). Modern examples of apparent movement are electronic signs like the one in **Figure 5.13**, which display moving advertisements or news headlines and movies. The perception of movement in these displays is so compelling that it is difficult to imagine that they are made up of stationary lights flashing on and off (for the news headlines) or still images flashed one after another (for the movies).

Wertheimer drew two conclusions from the phenomenon of apparent movement. His first conclusion was that apparent movement can't be explained by sensations alone, because there is nothing in the dark space between the flashing lights. His second conclusion, which became one of the basic principles of Gestalt psychology, is *the whole is different than the sum of its parts*, because the perceptual system creates the perception of movement where there actually is none. The idea that the whole is different than the sum of its parts became the battle cry of the Gestalt psychologists. "Wholes" were in; "sensations" were out (see page 5 for more on sensations).

Illusory Contours Another demonstration that argues against sensations and for the idea that the whole is different than the sum of its parts is shown in **Figure 5.14**. This demonstration involves circles with a "mouth" cut out, which resemble "Pac Man" figures from the classic video game introduced in the 1980s. We begin with the Pac Men in **Figure 5.14a**. You may see an edge running between the "mouths" of the Pac Men, but if you cover up one of them, the edge vanishes. This single edge becomes part of a triangle when we add the third Pac Man, in **Figure 5.14b**. The three Pac Men have created the perception of a triangle, which becomes more obvious by adding lines, as shown in **Figure 5.14c**. The edges that create

Corbis Bridge/Alamy Stock Photo

Figure 5.13 The stock ticker in Times Square, New York. The letters and numbers that appear to be moving smoothly across the screen are created by hundreds of small lights that are flashing on and off.

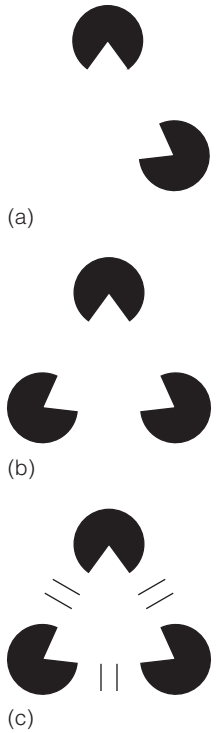

Figure 5.14 The illusory contours clearly visible in (b) and (c) cannot be caused by sensations, because there is only white there.

the triangle are called illusory contours because there are actually no physical edges present. Sensations can't explain illusory contours, because there aren't any sensations along the contours. The idea that the whole is different than the sum of its parts led the Gestalt psychologists to propose a number of *principles of perceptual organization* to explain the way elements are grouped together to create larger objects.

Gestalt Principles of Perceptual Organization

Having questioned the idea that perceptions are created by adding up sensations, the Gestalt psychologists proposed that perception depends on a number of principles of perceptual organization, which determine how elements in a scene become grouped together. The starting points for the principles of organization are things that usually occur in the environment. Consider, for example, how you perceive the rope in **Figure 5.15a**. Although there are many places where one strand is overlapped by another strand, you probably perceive the rope not as a number of separate pieces but as a continuous strand, as illustrated by the highlighted segment of rope in **Figure 5.15b**. The Gestalt psychologists, being keen observers of perception, used this kind of observation to formulate the *principle of good continuation*.

Good Continuation The principle of good continuation states the following: *Points that, when connected, result in straight or smoothly curving lines are seen as belonging together, and the lines tend*

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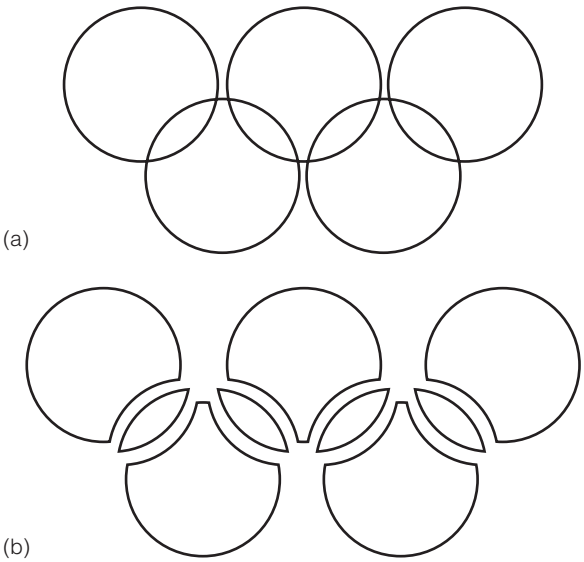
(a) (b)

Figure 5.15 (a) Rope on the beach. (b) Good continuation helps us perceive the rope as a single strand.

to be seen in such a way as to follow the smoothest path. The wire starting at A in **Figure 5.16** flowing smoothly to B is an example of lines following the smoothest path. The path from A does not go to C or D because those paths would violate good continuation by making sharp turns. The principle of good continuation also states that *objects that are partially covered by other objects are seen as continuing behind the covering object*. The rope in Figure 5.15 illustrates how covered objects are seen as continuing behind the object that covers them.

Pragnanz Pragnanz, roughly translated from the German, means "good figure." The **principle of pragnanz**, also called the **principle of good figure** or the **principle of simplicity**, states: *Every stimulus pattern is seen in such a way that the resulting structure is as simple as possible*. The familiar Olympic symbol in **Figure 5.17a** is an example of the principle of simplicity at work. We see this display as five circles and not as a larger number of more complicated shapes such as the ones in the "exploded view" of the Olympic symbol in **Figure 5.17b**. The principle of good continuation also contributes to perceiving the five circles. Can you see why this is so?



(a) (b)

Figure 5.17 (a) The Olympic symbol is perceived as five circles, not as the nine shapes in (b).

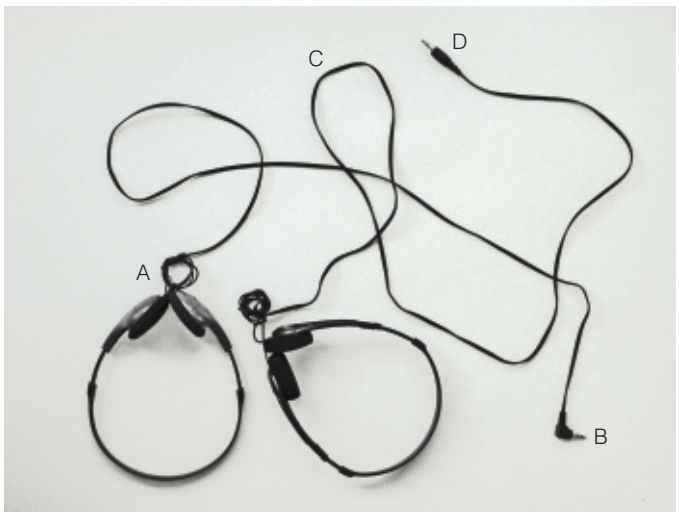
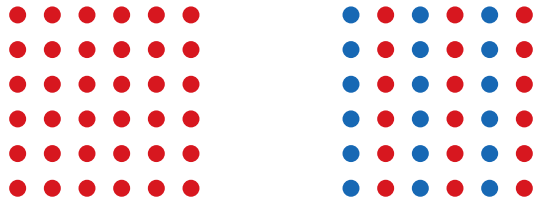


Figure 5.16 Good continuation helps us perceive two separate wires, even though they overlap.

Similarity Most people perceive **Figure 5.18a** as either horizontal rows of circles, vertical columns of circles, or a square



(a) (b)

Figure 5.18 (a) These dots are perceived as horizontal rows or vertical columns or both. (b) These dots are perceived as vertical columns.

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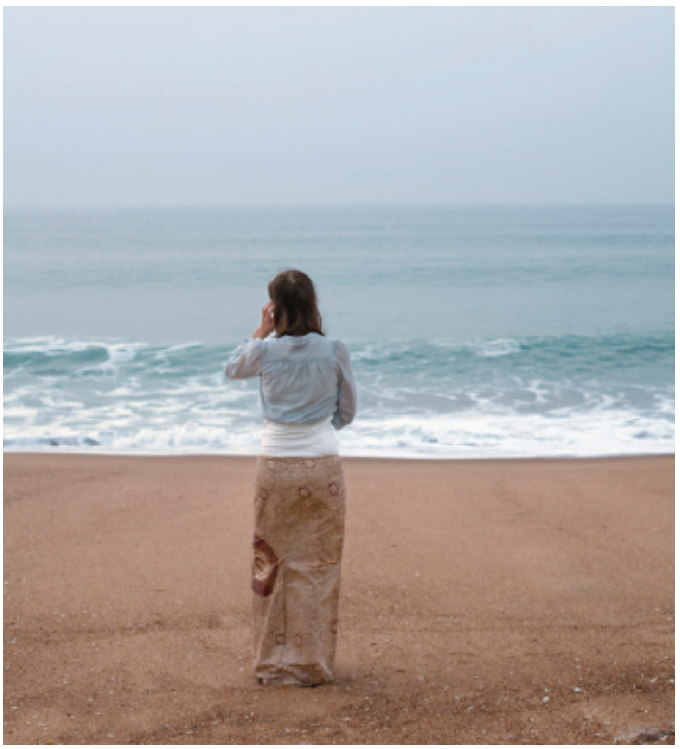
filled with evenly spaced dots. But when we change the color of some of the columns, as in **Figure 5.18b**, most people perceive vertical columns of circles. This perception illustrates the principle of similarity: *Similar things appear to be grouped together*. This law causes circles of the same color to be grouped together. A striking example of grouping by similarity of color is shown in **Figure 5.19**. Grouping can also occur because of similarity of shape, size, or orientation.

Grouping also occurs for auditory stimuli. For example, notes that have similar pitches and that follow each other closely in time can become perceptually grouped to form a melody. We will consider this and other auditory grouping effects when we describe organizational processes in hearing in Chapter 12 and perceiving music in Chapter 13.

Proximity (Nearness) Our perception of **Figure 5.20** as three groups of candles illustrates the principle of proximity, or nearness: *Things that are near each other appear to be grouped together*.

Common Fate According to the principle of common fate, *things that are moving in the same direction appear to be grouped together*. Thus, when you see a flock of hundreds of birds all flying together, you tend to see the flock as a unit; if some of the birds start flying in another direction, this creates a new unit. Note that common fate can work even if the objects in a group are dissimilar. The key to common fate is that a group of objects is moving in the same direction.



Wilma Hurskainen

Figure 5.19 This photograph, *Waves*, by Wilma Hurskainen, was taken at the exact moment that the front of the white water aligned with the white area on the woman's clothing. Similarity of color causes grouping; differently colored areas of the dress are perceptually grouped with the same colors in the scene. Also notice how the front edge of the water creates grouping by good continuation across the woman's dress.

Bruce Goldstein

Figure 5.20 The candles are grouped by proximity to create three separate groups. Can you identify additional Gestalt principles in the patterns on the menorah?

Common fate can apply not only to changes in spatial position, as the original Gestalt psychologists proposed, but also to changes in illumination when elements of our visual field that become lighter or darker simultaneously are perceived as being grouped into a unit (Sekuler & Bennett, 2001). For example, if you're at a rock concert and some of the stage lights are flickering on and off at the same time, you might perceive them as one group.

The principles we have just described were proposed by the Gestalt psychologists in the early 1900s. The following additional principles have been proposed by modern perceptual psychologists.

Common Region **Figure 5.21a** illustrates the principle of common region: *Elements that are within the same region of space appear to be grouped together*. Even though the circles inside the ovals are farther apart than the circles that are next to each other in neighboring ovals, we see the circles inside the ovals as belonging together. This occurs because each oval is seen as a separate region of space (Palmer, 1992; Palmer & Rock, 1994). Notice that in this example, common region overpowers proximity, because proximity would predict that the nearby circles would be perceived together. But even though the circles that are in different regions are close to each other in space, they do not group with each other, as they did in Figure 5.20.

Uniform Connectedness According to the principle of uniform connectedness, *a connected region of the same visual properties, such as lightness, color, texture, or motion, is perceived as a single unit* (Palmer & Rock, 1994). For example, in **Figure 5.21b**, the connected circles are perceived as grouped together, just as they were when they were in the same region in Figure 5.21a. Again, connectedness overpowers proximity.

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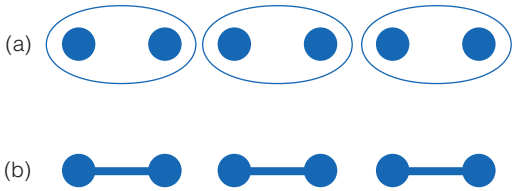

Figure 5.21 Grouping by (a) common region and (b) uniform connectedness.

The Gestalt principles we have described predict what we will perceive, based on what usually happens in the environment. Many of my students react to this idea by saying that the Gestalt principles therefore aren't anything special, because all they are doing is describing the obvious things we see every day. When they say this, I remind them that the reason we perceive scenes like the city buildings in Figure 5.1 or the scene in **Figure 5.22** so easily is that we use observations about commonly occurring properties of the environment to organize the scene. Thus, we assume, without even thinking about it, that the men's legs in Figure 5.22 extend behind the gray boards, because generally in the environment when two visible parts of an object (like the men's legs) have the same color and are "lined up," they belong to the same object and extend behind whatever is blocking it.

People don't usually think about how we perceive situations like this as being based on assumptions or predictions, but that is, in fact, what is happening—an idea that we'll return to later in the chapter. The reason the "assumption" seems so obvious is that we have had so much experience with things like this in the environment. That the "assumption" is actually almost a "sure thing" may cause us to take the Gestalt principles for granted and label them as "obvious." But the reality is that the Gestalt principles are nothing less than the basic operating characteristics of our visual system that determine how our perceptual system organizes elements of the environment into larger units.

Bruce Goldstein

Figure 5.22 A usual occurrence in the environment: Objects (the men's legs) are partially hidden by another object (the gray boards). In this example, the men's legs continue in a straight line and are the same color above and below the boards, so it is highly likely that they continue behind the boards.

Perceptual Segregation

The Gestalt psychologists were also interested in determining characteristics of the environment responsible for perceptual segregation—the perceptual separation of one object from another, as occurred when you saw the buildings in Figure 5.1 as separate from one another. One approach to studying perceptual segregation is to consider the problem of **figure–ground segregation**. When we see a separate object, it is usually seen as a **figure** that stands out from its background, which is called the **ground**. For example, sitting at your desk, you would probably see a book or papers on your desk as figure and the surface of your desk as ground, or stepping back from the desk, you might see the desk as figure and the wall behind it as ground. The Gestalt psychologists were interested in determining the properties of the figure and the ground and what causes us to perceive one area as figure and the other as ground.

Properties of Figure and Ground One way the Gestalt psychologists studied the properties of figure and ground was by considering patterns like the one in **Figure 5.23**, which was introduced by Danish psychologist Edgar Rubin in 1915. This pattern is an example of **reversible figure–ground** because it can be perceived alternately either as two dark blue faces looking at each other, in front of a gray background, or as a gray vase on a dark blue background. Some of the properties of the figure and ground are:

- The figure is more "thinglike" and more memorable than the ground. Thus, when you see the vase as figure, it appears as an object that can be remembered later. However, when you see the same light area as ground, it does not appear to be an object but is just "background" and is therefore not particularly memorable.

Figure 5.23 A version of Rubin's reversible face–vase figure.

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(a) (b)

Figure 5.24 (a) When the vase is perceived as figure, it is seen in front of a homogeneous dark background. (b) When the faces are seen as figure, they are seen in front of a homogeneous light background.

- The figure is seen as being in front of the ground. Thus, when the vase is seen as figure, it appears to be in front of the dark background (**Figure 5.24a**), and when the faces are seen as figure, they are on top of the light background (**Figure 5.24b**).
- Near the borders it shares with the figure, the ground is seen as unformed material, without a specific shape, and seems to extend behind the figure. This is not to say that grounds lack shape entirely. Grounds are often shaped by borders distant from those they share with the figure; for instance, the backgrounds in **Figure 5.24** are rectangles.
- The border separating the figure from the ground appears to belong to the figure. Consider, for example, the Rubin face–vase in Figure 5.23. When the two faces are seen as figure, the border separating the blue faces from the grey background belongs to the faces. This property of the border belonging to one area is called border ownership. When perception shifts so the vase is perceived as figure, border ownership shifts as well, so now the border belongs to the vase.

Properties of the Image That Determine Which Area Is Figure In an image like the Rubin face–vase in Figure 5.23, how does your visual system decide which region "owns" the border and is therefore perceived as the figure? To answer this, we return to the Gestalt psychologists, who specified a number of figural cues within the image that determine which areas are perceived as figure. These Gestalt figural cues are not to be confused with the Gestalt principles of perceptual organization; while the principles of organization determine how elements of an image are *grouped together*, figural cues determine how an image is *segregated* into figure and ground.

One figural cue proposed by the Gestalt psychologists was that areas lower in the field of view are more likely to be perceived as figure (Ehrenstein, 1930; Koffka, 1935). This idea was confirmed experimentally years later by Shaun Vecera and coworkers (2002), who briefly flashed stimuli like the ones in **Figure 5.25a** and determined which area was seen as figure, the red area or the green area. The results, shown in **Figure 5.25b**, indicate that for the upper–lower displays, observers were more likely to perceive the lower area as figure, but for the left–right displays, they showed only a small preference for the left region. From this result, Vecera concluded that

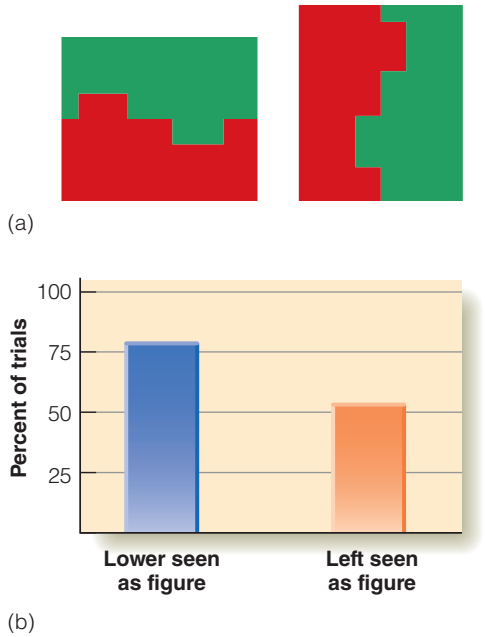

Figure 5.25 (a) Stimuli from the Vecera et al. (2002) experiment. (b) Percentage of trials on which lower or left areas were seen as figure.

there is a preference for seeing objects lower in the display as figure. This conclusion makes sense when we consider a scene like the one in **Figure 5.26**, in which the lower part of the scene is figure and the sky is ground. What is significant about this scene is that it is typical of scenes we perceive every day. In our normal experience, the "figure" is much more likely to be below the horizon.

Another Gestalt proposal was that figures are more likely to be perceived on the convex side of borders (borders that bulge outward) (Kanizsa & Gerbino, 1976). Mary Peterson and Elizabeth Salvagio (2008) demonstrated this by presenting

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Figure 5.26 The field, in the bottom half of the visual field, is seen as figure. The sky, in the upper half of the visual field, is seen as ground.

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(a) (b) (c)

Figure 5.27 Stimuli from Peterson and Salvagio's (2008) experiment: (a) 8-component display; (b) 2-component display; (c) 4-component display. The red squares appeared on different areas on different trials. The participant's task was to judge whether the red square was "on" or "off" the area perceived as figure.

displays like the one in **Figure 5.27a** and asking observers to indicate whether the red square was "on" or "off" the area perceived as figure. Thus, if they perceived the dark area in this example as being a figure, they would say "on." If they perceived the dark area as ground, they would say "off." The result, in agreement with the Gestalt proposal, was that convex regions, like the dark regions in Figure 5.27a, were perceived as figure 89 percent of the time.

But Peterson and Salvagio went beyond simply confirming the Gestalt proposals by also presenting displays like the ones in **Figures 5.27b** and **5.27c**, which had fewer components. Doing this greatly decreased the likelihood that convex displays would be seen as figure, with the black convex region in the two-component display (Figure 5.27b) being seen as figure only 58 percent of the time. What this result means, according to Peterson and Salvagio, is that to understand how segregation occurs we need to go beyond simply identifying factors like convexity. Apparently, segregation is determined not by just what is happening at a single border but by what is happening in the wider scene. This makes sense when we consider that perception generally occurs in scenes that extend over a wide area. We will return to this idea later in the chapter when we consider how we perceive scenes.

The Role of Perceptual Principles and Experience in Determining Which Area Is Figure The Gestalt psychologists' emphasis on perceptual principles led them to minimize the role of a person's past experiences in determining perception. They believed that although perception can be affected by experience, built-in principles can override experience. The Gestalt psychologist Max Wertheimer (1912) provided the following example to illustrate how built-in principles could override experience: Most people recognize the display in **Figure 5.28a** as a "W" sitting on top of an "M," largely because of our past experiences with those two letters. However, when the letters are arranged as in **Figure 5.28b**, most people see two uprights plus a pattern in between them. The uprights, which are created by the principle of good continuation, are the dominant perception and override the effects of past experience with *W*s or *M*s.

The Gestalt idea that past experience and the meanings of stimuli (like the *W* and *M*) play a minor role in perceptual

(a) (b)

Figure 5.28 (a) *W* on top of *M*. (b) When combined, a new pattern emerges, overriding the meaningful letters. (From Wertheimer, 1912)

organization is also illustrated by the Gestalt proposal that one of the first things that occurs in the perceptual process is the segregation of figure from ground. They contended that the figure must stand out from the ground before it can be recognized. In other words, the figure has to be separated from the ground before we can assign a meaning to the figure.

But Bradley Gibson and Mary Peterson (1994) did an experiment that argued against this idea by showing that figure–ground formation can be affected by the meaningfulness of a stimulus. They demonstrated this by presenting a display like the one in **Figure 5.29a**, which can be perceived in two ways: (1) a standing woman (the black part of the display) or (2) a less meaningful shape (the white part of the display). When they presented stimuli such as this for a fraction of a second and asked observers which region seemed to be the figure, they found that observers were more likely to say that the meaningful part of the display (the woman, in this example) was the figure.

Why were the observers more likely to perceive the woman? One possibility is that they recognized that the black area was a familiar object. In fact, when Gibson and Peterson turned the display upside down, as in **Figure 5.29b**, so that it was more difficult to recognize the black area as a woman, participants were less likely to see that area as being the figure. The fact that meaningfulness can influence the assignment of an area as figure means that the process of recognition must be occurring

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(a) (b)

Figure 5.29 Gibson and Peterson's (1994) stimulus. (a) The black area is more likely to be seen as figure because it is meaningful. (b) This effect does not occur when meaningfulness is decreased by turning the picture upside down.

either before or at the same time as the figure is being separated from the ground (Peterson, 1994, 2001, 2019).

So far, the principles and research we have been describing have focused largely on how our perception of individual objects depends on organizing principles and principles that determine which parts of a display will be seen as figure and which will be seen as ground. If you look back at the illustrations in this section, you will notice that most of them are simple displays designed to illustrate a specific principle of perceptual organization. In the next section, we'll consider a more modern approach to object perception called *recognition-by-components theory*.

TEST YOURSELF 5.1

1. What are some of the problems that make object perception difficult for computers but not for humans?
2. What is structuralism, and why did the Gestalt psychologists propose an alternative to this way of explaining perception?
3. How did the Gestalt psychologists explain perceptual organization?
4. How did the Gestalt psychologists describe figure–ground segregation? What are some basic properties of figure and ground?
5. What properties of a stimulus tend to favor perceiving an area as "figure"? Be sure you understand Vecera's experiment that showed that the lower region of a display tends to be perceived as figure, and why Peterson and Salvagio stated that to understand how segregation occurs we have to consider what is happening in the wider scene.
6. Describe the Gestalt ideas about the role of meaning and past experience in determining figure–ground segregation.
7. Describe Gibson and Peterson's experiment that showed that meaning can play a role in figure–ground segregation.

5.3 Recognition by Components

In the previous section, we discussed how we organize a visual image by grouping elements of that image into coherent units and by separating objects from their backgrounds. Now, we'll move from organization to recognition and discuss how we recognize those individual objects. For instance, how do you recognize the black region in Figure 5.29a as a silhouette of a woman?

A theory of object recognition called **recognition by components (RBC) theory** was proposed by Irving Biederman in the 1980s (Biederman, 1987). RBC theory states that objects are comprised of individual geometric components called **geons**, and we recognize objects based on the arrangement of those geons. Geons are three-dimensional shapes, like pyramids, cubes, and cylinders. **Figure 5.30a** shows some examples of geons, but this is just a small sample; Biederman proposed that there are 36 different geons from which most objects we encounter can be assembled and recognized. Geons are the building blocks of objects and the same geons can be arranged in different ways to form different objects, as illustrated in **Figure 5.30b**. For instance, the cylinder could be part of the mug or the base of the lamp.

An important aspect of the RBC theory is that it accounts for viewpoint invariance, the fact that a given object can be recognized from different viewpoints. RBC theory accounts for this because even if the mug in Figure 5.30b was viewed from the side rather than from the front, it is still comprised of the same geons, so it is still recognized as a mug.

RBC theory provided a simple and elegant way of approaching object perception that included viewpoint invariance. However, there are many aspects of object perception that the RBC theory could not explain. For instance, it doesn't account for grouping or organization like the Gestalt principles do, and some objects simply can't be represented by assemblies of geons (like clouds in the sky that typically don't have geometric components). The RBC theory also doesn't allow for distinguishing between objects within a given category, such as two different types of coffee mugs or species of birds that might be composed of the same basic shapes. Thus, while

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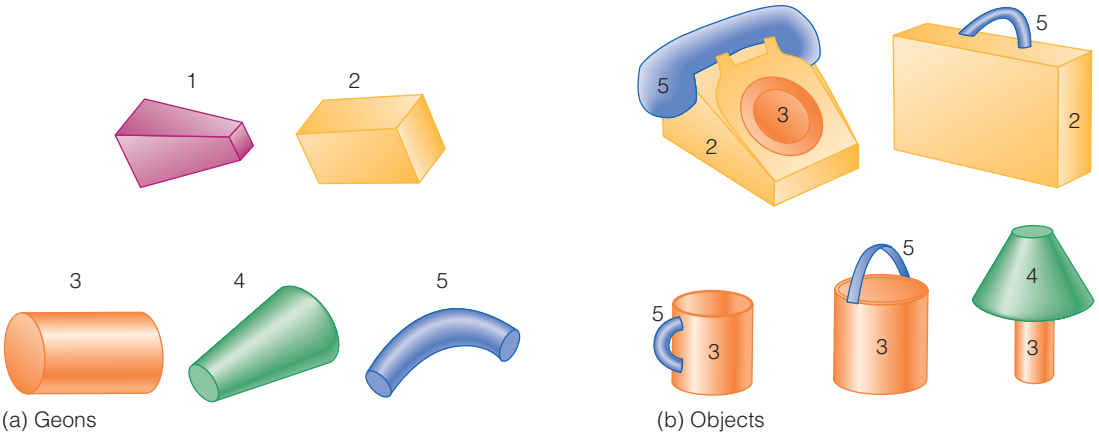

Figure 5.30 (a) Some geons. (b) Some objects created from these geons. The numbers on the objects indicate which geons are present. Note that recognizable objects can be formed by combining just two or three geons. Also note that the relations between the geons matter, as illustrated by the cup and the pail. (Biederman, 1987)

the RBC theory played its role in history in that it got people thinking about how the visual system represents objects, research in the field has moved on to consider objects not just as a collection of geometric components, but also as part of more meaningful, real-world scenes.

5.4 Perceiving Scenes and Objects in Scenes

A **scene** is a view of a real-world environment that contains (1) background elements and (2) multiple objects that are organized in a meaningful way relative to each other and the background (Epstein, 2005; Henderson & Hollingworth, 1999). One way of distinguishing between objects and scenes is that objects are compact and are *acted upon*, whereas scenes are extended in space and are *acted within*. For example, if we are walking down the street and mail a letter, we would be *acting upon* the mailbox (an object) and *acting within* the street (the scene).

Perceiving the Gist of a Scene

Perceiving scenes presents a paradox. On one hand, scenes are often large and complex. However, despite this size and complexity, you can identify important properties of most scenes after viewing them for only a fraction of a second. This general description of the type of scene is called the **gist of a scene**. An example of your ability to rapidly perceive the gist of a scene is the way you can rapidly flip from one TV channel to another, yet still grasp the meaning of each picture as it flashes by—a car chase, quiz contestants, or an outdoor scene with mountains—even though you may be seeing each picture for a second or less and so may not be able to identify specific objects. When you do this, you are perceiving the gist of each scene (Oliva & Torralba, 2006).

Exactly how long does it take to perceive the gist of a scene? Mary Potter (1976) showed observers a target picture and then asked them to indicate whether they saw that picture as they viewed a sequence of 16 rapidly presented pictures. Her observers could do this with almost 100 percent accuracy even when the pictures were flashed for only 250 ms (ms = milliseconds; 250 ms = 1/4 second). Even when the target picture was only specified by a written description, such as "girl clapping," observers achieved an accuracy of almost 90 percent (**Figure 5.31**).

Another approach to determining how rapidly people can perceive scenes was used by Li Fei-Fei and coworkers (2007), who presented pictures of scenes for exposures ranging from 27 ms to 500 ms and asked observers to write a description

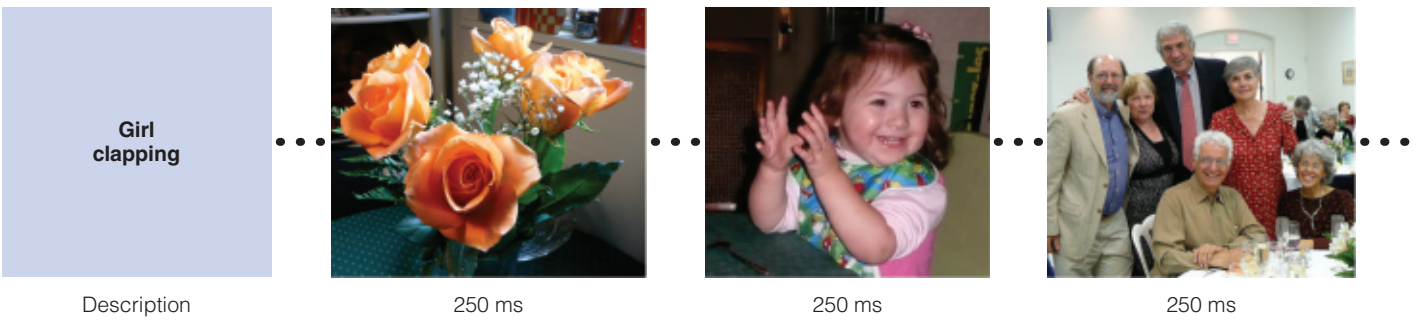

Figure 5.31 Procedure for Potter's (1976) experiment. She first presented either a target photograph or, as shown here, a description, and then rapidly presented 16 pictures for 250 ms each. The observer's task was to indicate whether the target picture had been presented. In this example, only 3 of the 16 pictures are shown, with the target picture being the second one presented. On some trials, the target picture was not included in the series of 16 pictures.

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of what they saw. This method of determining the observer's response is a nice example of the phenomenological report, described in Chapter 1 (p. 17). Fei-Fei used a procedure called *masking* to be sure the observers saw the pictures for exactly the desired duration.

METHOD | Using a Mask to Achieve Brief Stimulus Presentations

What if we want to present a stimulus that is visible for only 100 ms? Although you might think that the way to do this would be to flash a stimulus for 100 ms, this won't work because of a phenomenon called persistence of vision—the perception of a visual stimulus continues for about 250 ms (1/4 second) after the stimulus is extinguished. Thus, a picture that is presented for 100 ms will be *perceived* as lasting about 350 ms. But the persistence of vision can be eliminated by presenting a visual masking stimulus, usually a random pattern that covers the original stimulus, so if a picture is flashed for 100 ms followed immediately by a masking stimulus, the picture is visible for just 100 ms. A masking stimulus is therefore often presented immediately after a test stimulus to stop the persistence of vision from increasing the duration of the test stimulus.

Typical results of Fei-Fei's experiment are shown in **Figure 5.32**. At brief durations, observers saw only light and dark areas of the pictures. By 67 ms they could identify some large objects (a person, a table), and when the duration was increased to 500 ms (half a second) they were able to identify smaller objects and details (the boy, the laptop). For a picture of an ornate 1800s living room, observers were able to identify the picture as a room in a house at 67 ms and to identify details, such as chairs and portraits, at 500 ms. Thus, the overall gist of the scene is perceived first, followed by perception of details and smaller objects within the scene.

Alice O'Donnell

27 ms	Looked like something black in the center with four straight lines coming out of it against a white background. (Subject: AM)
40 ms	The first thing I could recognize was a dark splotch in the middle. It may have been rectangular-shaped, with a curved top... but that's just a guess. (Subject: KM)
67 ms	A person, I think, sitting down or crouching. Facing the left side of the picture. We see their profile mostly. They were at a table or where some object was in front of them (to their left side in the picture). (Subject: EC)
500 ms	This looks like a father or somebody helping a little boy. The man had something in his hands, like an LCD screen or a laptop. They looked like they were standing in a cubicle. (Subject: WC)

Figure 5.32 Observer's description of a photograph presented in Fei-Fei's (2007) experiment. Viewing durations are indicated on the left. (From Fei-Fei et al., 2007)

What enables observers to perceive the gist of a scene so rapidly? Aude Oliva and Antonio Torralba (2001, 2006) propose that observers use information called **global image features**, which can be perceived rapidly and are associated with specific types of scenes. Some of the global image features proposed by Oliva and Torralba are:

- *Degree of naturalness*. Natural scenes, such as the ocean and forest in **Figure 5.33**, have textured zones and undulating contours. Man-made scenes, such as the street, are dominated by straight lines and horizontals and verticals.
- *Degree of openness*. Open scenes, such as the ocean, often have a visible horizon line and contain few objects. The street scene is also open, although not as much as the ocean scene. The forest is an example of a scene with a low degree of openness.
- *Degree of roughness*. Smooth scenes (low roughness) like the ocean contain fewer small elements. Scenes with high roughness like the forest contain many small elements and are more complex.
- *Degree of expansion*. The convergence of parallel lines, like what you see when you look down railroad tracks that appear to vanish in the distance, or in the street scene in Figure 5.33, indicates a high degree of expansion. This feature is especially dependent on the observer's viewpoint. For example, in the street scene, looking directly at the side of a building would result in low expansion.
- *Color*. Some scenes have characteristic colors, like the ocean scene (blue) and the forest (green and brown). (Castelhano & Henderson, 2008; Goffaux et al., 2005)

Global image features are *holistic* and *rapidly perceived*. They are properties of the scene as a whole and do not depend on time-consuming processes such as perceiving small details, recognizing individual objects, or separating one object from another. Another property of global image features is that they contain information about a scene's structure and spatial layout. For example, the degree of openness and the degree of expansion refer directly to characteristics of a scene's layout; naturalness also provides layout information that comes from knowing whether a scene is from nature or contains human-made structures.

Global image properties not only help explain how we can perceive the gist of scenes based on features that can be seen in brief exposures, they also illustrate the following general property of perception: Our past experiences in perceiving properties of the environment play a role in determining our perceptions. We learn, for example, that blue is associated with open sky, that landscapes are often green and smooth, and that verticals and horizontals are associated with buildings. Characteristics of the environment such as this, which occur

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Figure 5.33 Three scenes that have different global image properties. See text for description.

frequently, are called regularities in the environment. We will now describe these regularities in more detail.

Regularities in the Environment: Information for Perceiving

Modern perceptual psychologists have introduced the idea that perception is influenced by two types of regularities: *physical regularities* and *semantic regularities*.

Physical Regularities Physical regularities are regularly occurring physical properties of the environment. For example, there are more vertical and horizontal orientations in the environment than oblique (angled) orientations. This occurs in human-made environments (for example, buildings contain many horizontals and verticals) and also in natural environments (trees and plants are more likely to be vertical or horizontal than slanted) (Coppola et al., 1998) (**Figure 5.34**). It is, therefore, no coincidence that people can perceive horizontals and verticals more easily than other orientations—the oblique effect we introduced in Chapter 1 (see page 12) (Appelle, 1972; Campbell et al., 1966; Orban et al., 1984). Another example of a physical regularity is that when one object partially covers another one, the contour of the partially covered object "comes out the other side," as occurs for the rope in Figure 5.15.

Yet another example is provided by the pictures in **Figure 5.35**. **Figure 5.35a** shows indentations created by people walking in the sand. But when we turn this picture upside down, as in **Figure 5.35b**, the indentations in the sand become rounded mounds. Our perception in these two situations has been explained by the light-from-above assumption: we usually assume that light is coming from above, because light in the environment, including the sun and most artificial light, usually comes from above (Kleffner & Ramachandran, 1992). **Figure 5.35c** shows how light coming from above and to the left illuminates an indentation, leaving a shadow on the left. **Figure 5.35d** shows how the same light illuminates a bump, leaving a shadow on the right. Our perception of illuminated shapes is influenced by how they are shaded, combined with the brain's assumption that light is coming from above.

One of the reasons humans are able to perceive and recognize objects and scenes so much better than computers is that our perceptual system is adapted to respond to physical characteristics of our environment, such as the orientation of objects and the direction of light. But this adaptation goes

Figure 5.34 In these two scenes from nature, horizontal and vertical orientations are more common than oblique orientations. These scenes are special examples, picked because the large proportion of verticals. However, randomly selected photos of natural scenes also contain more horizontal and vertical orientations than oblique orientations. This also occurs for human-made buildings and objects.

beyond physical characteristics. It also occurs because we have learned about what types of objects typically occur in specific types of scenes.

Semantic Regularities In language, *semantics* refers to the meanings of words or sentences. Applied to perceiving scenes, semantics refers to the meaning of a scene. This meaning is often related to what happens within a scene. For example, food preparation, cooking, and perhaps eating occur

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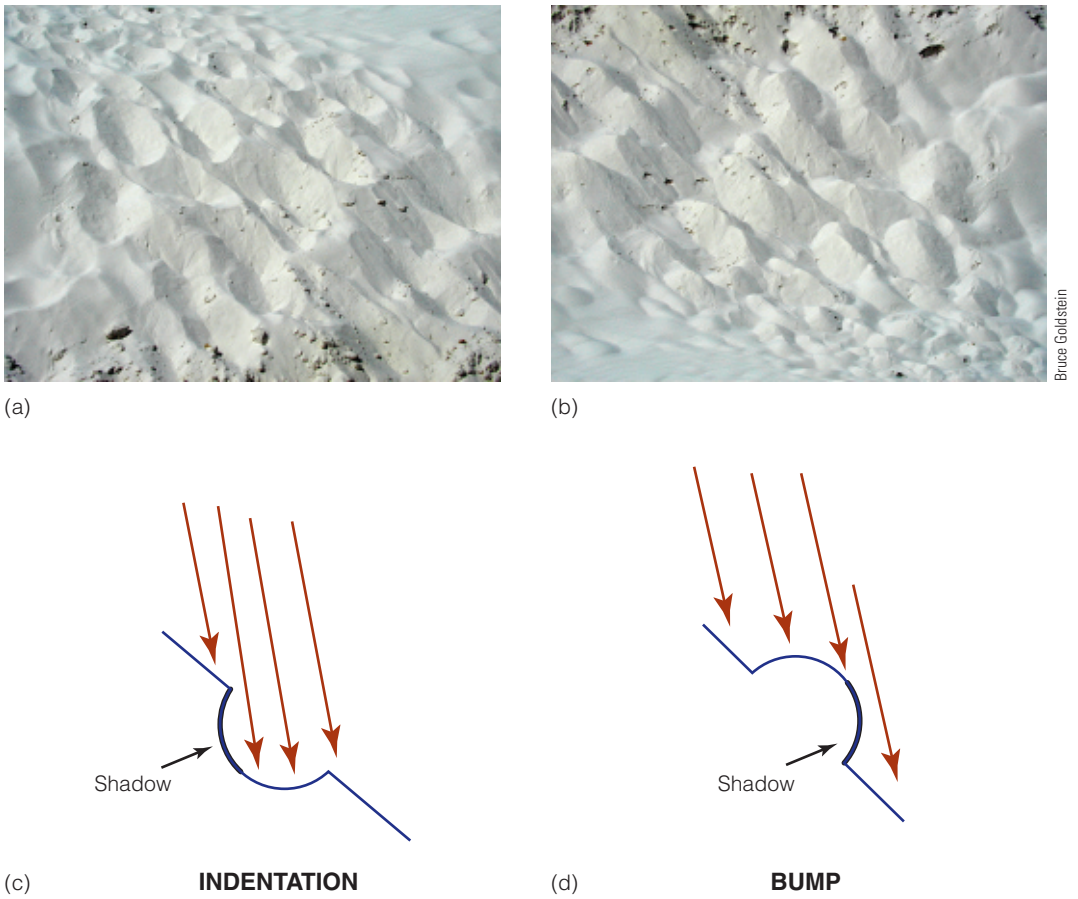

Figure 5.35 (a) Indentations made by people walking in the sand. (b) Turning the picture upside down turns indentations into rounded mounds. (c) How light from above and to the left illuminates an indentation, causing a shadow on the left. (d) The same light illuminating a bump causes a shadow on the right.

in a kitchen; waiting around, buying tickets, checking luggage, and going through security checkpoints happen in airports. **Semantic regularities** are the characteristics associated with activities that are common in different types of scenes.

One way to demonstrate that people are aware of semantic regularities is simply to ask them to imagine a particular type of scene or object, as in the following demonstration.

DEMONSTRATION | Visualizing Scenes and Objects

Your task in this demonstration is simple. Close your eyes and then visualize or simply think about the following scenes and objects:

1. An office
2. The clothing section of a department store
3. A microscope
4. A lion

Most people who have grown up in modern society have little trouble visualizing an office or the clothing section of a department store. What is important about this ability, for our purposes, is that part of this visualization involves details within these scenes. Most people see an office as having a desk with a computer on it, bookshelves, and a chair. The department store scene may contain racks of clothes, a changing room, and perhaps a cash register.

What did you see when you visualized the microscope or the lion? Many people report seeing not just a single object, but an object within a setting. Perhaps you perceived the microscope sitting on a lab bench or in a laboratory, and the lion in a forest or on a savannah or in a zoo. The point of this demonstration is that our visualizations contain information based on our knowledge of different kinds of scenes. This knowledge of what a given scene typically contains is called a **scene schema**.

An example of how a scene schema can influence perception is an experiment by Stephen Palmer (1975), which used stimuli like the picture in **Figure 5.36**. Palmer first presented a context scene such as the one on the left and then briefly flashed one of the target pictures on the right. When Palmer asked observers to identify the object in the target picture, they correctly identified an object like the loaf of bread (which is appropriate to the kitchen scene) 80 percent of the time, but correctly identified the mailbox or the drum (two objects that don't fit into the scene) only 40 percent of the time. Apparently, Palmer's observers were using their knowledge about kitchens to help them perceive the briefly flashed loaf of bread.

The effect of semantic regularities is also illustrated in **Figure 5.37**, which is called "the multiple personalities of a blob" (Oliva & Torralba, 2007). The blob (a) is perceived as different objects depending on its orientation and the context within which it is seen. It appears to be an object on a table

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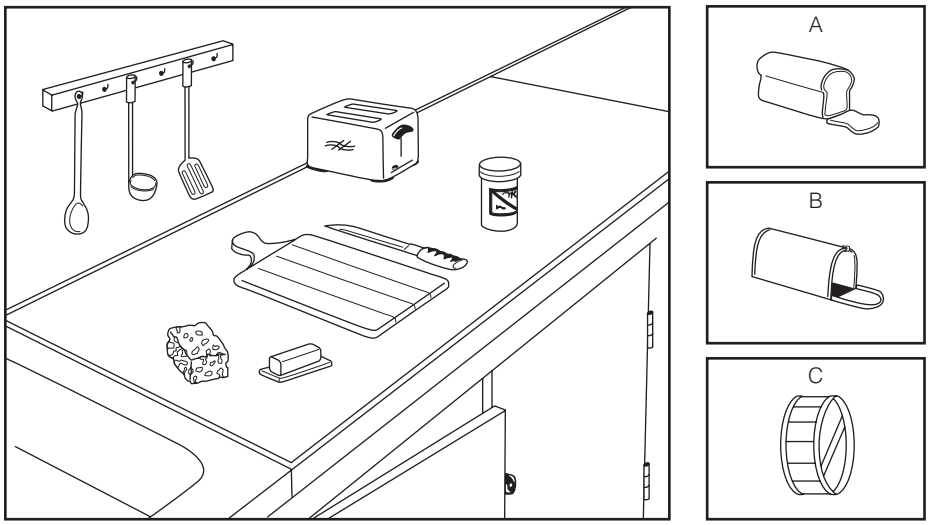

Figure 5.36 Stimuli used in Palmer's (1975) experiment. The scene at the left is presented first, and the observer is then asked to identify one of the rapidly flashed objects on the right.

in (b), a shoe on a person bending down in (c), and a car and a person crossing the street in (d), even though it is the same shape in all of the pictures.

Although people make use of regularities in the environment to help them perceive, they are often unaware of the specific information they are using. This aspect of perception is similar to what occurs when we use language. Even though people easily string words together to create sentences in conversations, they may not know the rules of grammar that specify how these words are being combined. Similarly, we easily use our knowledge of regularities in the environment to help us perceive, even though we may not be able to identify the specific information we are using.

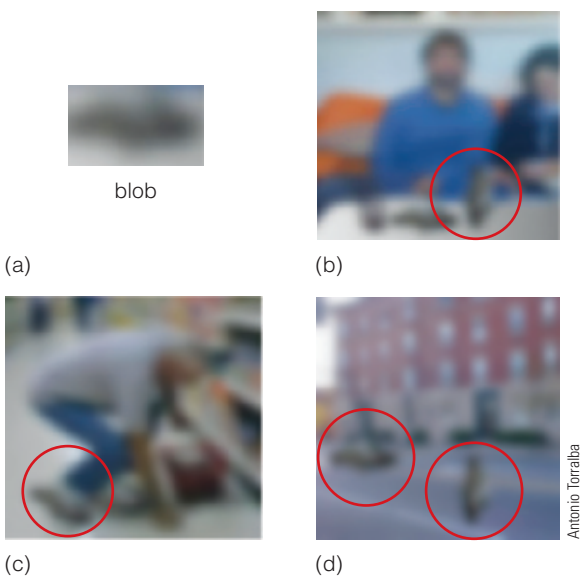

Figure 5.37 "Multiple personalities of a blob." What we expect to see in different contexts influences our interpretation of the identity of the "blob" inside the circles. (From Oliva & Torralba, 2007)

The Role of Inference in Perception

People use their knowledge of physical and semantic regularities such as the ones we have been describing to *infer* what is present in a scene. The idea that perception involves inference is nothing new; it was introduced in the 18th century by Hermann von Helmholtz (1866/1911), who proposed the *theory of unconscious inference*.

Helmholtz's Theory of Unconscious Inference

Helmholtz made many discoveries in physiology and physics, developed the ophthalmoscope (the device that an optometrist or ophthalmologist uses to look into your eyes), and proposed theories of object perception, color vision, and hearing. One of Helmholtz's contributions to perception was based on his realization that the image on the retina is ambiguous. We have seen that retinal ambiguity means that a particular pattern of stimulation on the retina can be caused by many different possible objects in the environment (see Figure 5.3). For example, what does the pattern of stimulation in **Figure 5.38a** represent? For most people, this pattern results in perception of a blue rectangle in front of a red rectangle, as shown in **Figure 5.38b**. But as **Figure 5.38c** indicates, this display could

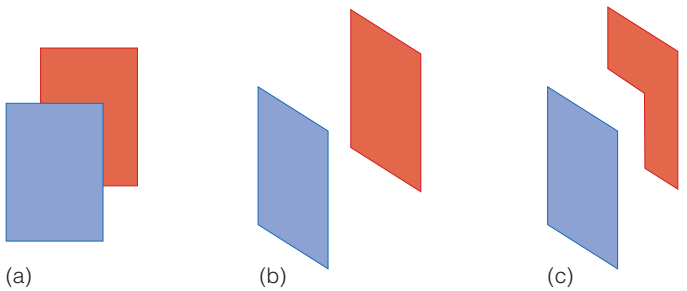

Figure 5.38 The display in (a) is usually interpreted as being (b) a blue rectangle in front of a red rectangle. It could, however, be (c) a blue rectangle and an appropriately positioned six-sided red figure.

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have been caused by a six-sided red shape positioned in front of, behind, or right next to the blue rectangle.

Helmholtz's question was, "How does the perceptual system 'decide' that this pattern on the retina was created by overlapping rectangles?" His answer was the **likelihood principle**, which states that we perceive the object that is *most likely* to have caused the pattern of stimuli we have received. This judgment of what is most likely occurs, according to Helmholtz, by a process called **unconscious inference**, in which our perceptions are the result of unconscious assumptions, or inferences, that we make about the environment. Thus, we *infer* that it is likely that Figure 5.38a is a rectangle covering another rectangle because of experiences we have had with similar situations in the past.

Helmholtz's description of the process of perception resembles the process involved in solving a problem. For perception, the problem is to determine which object caused a particular pattern of stimulation, and this problem is solved by a process in which the perceptual system uses the observer's knowledge of the environment to infer what the object might be.

The idea that inference is important for perception has recurred throughout the history of perception research in various forms. In modern research, Helmholtz's theory of unconscious inference has been reconceptualized as **prediction**—the idea that our past experiences help us make informed guesses about what we will perceive. But what, exactly, is the process by which we make predictions? One approach that provides insight into how predictions can be used in object perception is called Bayesian inference.

Bayesian Inference In 1763, Thomas Bayes proposed what is known as **Bayesian inference** (Geisler, 2008, 2011; Kersten et al., 2004; Yuille & Kersten, 2006). According to Bayes, our estimate of the probability of an outcome is determined by two factors: (1) the **prior probability**, or simply the **prior**, which is our initial estimate of the probability of an outcome, and (2) the extent to which the available evidence is consistent with the outcome. This second factor is called the **likelihood** of the outcome.

To illustrate Bayesian inference, let's first consider **Figure 5.39a**, which shows Maria's *priors* for three types of health problems. Maria believes that having a cold or heartburn is likely to occur, but having lung disease is less likely. With these priors in her head (along with lots of other beliefs about health-related matters), Maria notices that her friend Charles has a bad cough. She guesses that three possible causes could be a cold, heartburn, or lung disease. Looking further into possible causes, she does some research and finds that coughing is often associated with having either a cold or lung disease, but isn't associated with heartburn (**Figure 5.39b**). This additional information, which is the *likelihood*, is combined with Maria's *priors* to produce the conclusion that Charles probably has a cold (**Figure 5.39c**) (Tenenbaum et al., 2011). In practice, Bayesian inference involves a mathematical procedure in which the prior is multiplied by the likelihood to determine the probability of the outcome. Thus, people start with a prior, then use additional evidence to update the prior and reach a conclusion (Wolpert & Ghahramani, 2005).

Applying this idea to object perception, let's return to the inverse projection problem from Figure 5.3. Remember that the inverse projection problem occurs because a huge number of possible objects could be associated with a particular image on the retina. So the problem is how to determine what is "out there" that is causing a particular retinal image. Luckily, we don't have to rely only on the retinal image, because we come to most perceptual situations with prior probabilities based on our past experiences.

One of the *priors* you have in your head is that books are rectangular. Thus, when you look at a book on your desk, your initial belief is that it is likely that the book is rectangular. The *likelihood* that the book is rectangular is provided by additional evidence such as the book's retinal image, combined with your perception of the book's distance and the angle at which you are viewing the book. If this additional evidence is consistent with your prior that the book is rectangular, the likelihood is high and the perception "rectangular" is strengthened. Further testing by changing your viewing angle and distance can further strengthen the conclusion that the shape is a rectangle. Note that you aren't necessarily conscious of this testing process—it occurs automatically and rapidly. The important point about this process is that while the retinal image is still the starting point for perceiving the shape of the book, adding the person's prior beliefs reduces the possible shapes that could be causing that image.

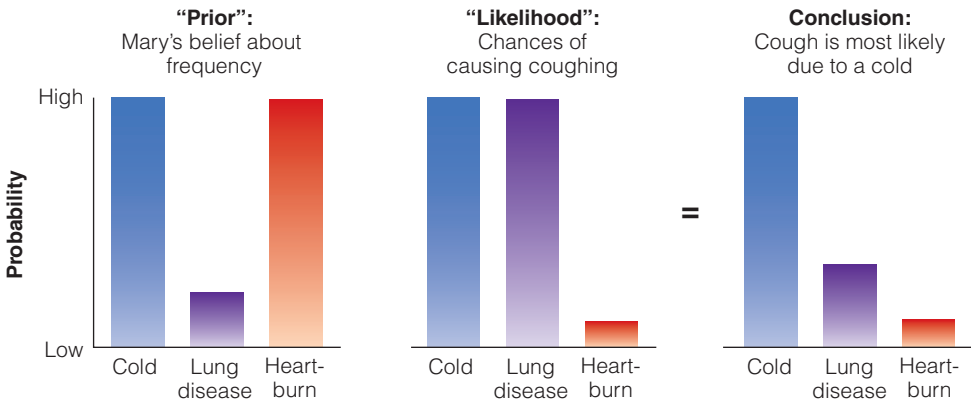

Figure 5.39 These graphs present hypothetical probabilities, to illustrate the principle behind Bayesian inference. (a) Maria's beliefs about the relative frequency of having a cold, lung disease, and heartburn. These beliefs are her *priors*. (b) Further data indicate that colds and lung disease are associated with coughing, but heartburn is not. These data contribute to the *likelihood*. (c) Taking the priors and likelihood together results in the conclusion that Charles's cough is probably due to a cold.

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What Bayesian inference does is to restate Helmholtz's idea that we perceive what is most likely to have created the stimulation we have received in terms of probabilities. It isn't always easy to specify these probabilities, particularly when considering complex perceptions. However, because Bayesian inference provides a specific procedure for determining what might be out there, researchers have used it to develop computer vision systems that can apply knowledge about the environment to more accurately translate the pattern of stimulation on their sensors into conclusions about the environment.

We've now discussed how our past experiences can be used to predict what is most likely to be "out there" in the world. But how does the brain actually implement these predictions? One recent theory—called *predictive coding*—provides an explanation.

How the Brain Implements Prediction

Predictive coding is a theory that describes how the brain uses our past experiences—or our "priors," as Bayes put it—to predict what we will perceive (Panichello et al., 2013; Rao & Ballard, 1999). This explanation begins by stating that our brain's predictions about the world are represented at higher levels of the visual system—for instance, toward the top of the "what" and "where/how" pathways introduced in Chapter 4, where the neurons respond to more complex information, like entire objects and scenes. According to predictive coding, when new incoming visual input reaches the receptors and is sent upward in the visual system, that signal is compared to the predictions flowing downward from higher levels (**Figure 5.40a**). In other words, the brain determines whether what we're seeing matches with what we *expect* to be seeing. If the incoming signal matches the higher-level prediction, nothing happens, as in (a). However, if the incoming signal doesn't match the prediction, then a prediction error signal is generated, which is sent back up to higher levels so that the existing prediction can be modified (**Figure 5.40b**). In this way, our current experiences can change existing representations in the brain in order to make better predictions and "learn" what to expect.

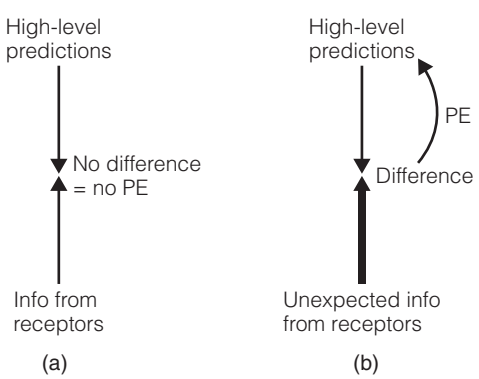

Figure 5.40 The general idea behind predictive coding. (a) Information from the receptors flows upward and is compared to the brain's predictions about what we expect to perceive, flowing downward from higher levels. If there is no difference between the signal from the receptors and the high-level predictions, then there is no prediction error (PE). (b) When something unexpected happens, the receptor information does not match the brain's predictions, and a prediction error signal is sent upward to make corrections to the predictions.

As an example of how predictive coding works in the real world, let's say you're walking across campus to get to class, and everything is as expected—there's nothing odd or out of place in your visual scene. In this case, your incoming visual input closely matches your brain's predictions of what you should be seeing, based on the many times you've walked that same path before, so there is no prediction error signal (Figure 5.40a). But now, let's say a chicken jumps out of the bushes and runs across your path. You've never seen a chicken on campus before, so that visual information does not match your brain's expectations, and an error signal is generated and sent to higher levels of the visual system (Figure 5.40b). Now, your brain's representation of campus has been updated to reflect the possibility of a chicken passing through. This is a good thing, because now you're more likely to be on the lookout for a rogue chicken the next time you walk that path, which ultimately may make you better able to respond to that situation, should it arise again.

Predictive coding is similar to Helmholtz's idea that we use our past experiences to make inferences about what we will perceive. But predictive coding takes unconscious inference a step further by linking prediction to what is happening in the brain. The idea that the brain makes predictions is an important concept that has become prominent in recent perception research—not only for object perception, but for other types of perception as well. One example, which we will consider later, is taste perception. If you expect a certain flavor—like chamomile tea, because that's what you ordered at the coffee shop—but the taste of coffee hits your tongue instead, you'd probably be surprised, which for your brain, would create an error signal, since the prediction did not match the experience.

We'll continue to see other examples illustrating the importance of prediction in later chapters. As we've discussed it here, though, predictive coding doesn't provide the details about what is happening in the brain. In the next section we will look at what we know about neural responding to objects and scenes.

TEST YOURSELF 5.2

1. What is the recognition by components theory? How does it account for viewpoint invariance?
2. What is the evidence that we can perceive the gist of a scene very rapidly? What information helps us identify the gist?
3. What are regularities in the environment? Give examples of physical regularities, and discuss how these regularities are related to the Gestalt laws of organization.
4. What are semantic regularities? How do semantic regularities affect our perception of objects within scenes? What is the relation between semantic regularities and the scene schema?

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5. Describe Helmholtz's theory of unconscious inference. What does this have to say about inference and perception?
6. Describe Bayesian inference. Be sure you understand the "sickness" example in Figure 5.39 and how Bayesian inference can be applied to object perception.
7. What is predictive coding? Describe an example of how the brain might use prediction to perceive a real-world situation.

5.5 Connecting Neural Activity and Object/Scene Perception

We look around. We see objects arranged in space, which creates a scene. So far in our discussion of objects and scenes, we have focused on how perception is determined by aspects of *stimuli*. We now consider the neural side of object and scene perception. Recall that in Chapter 4, we discussed how single-cell recording studies in monkeys have shown that certain neurons, grouped together into a certain area within the temporal lobe, can respond to specific complex stimuli, like faces. But what about in humans? How do our brains respond when we perceive faces, objects, and scenes?

Brain Responses to Objects and Faces

In the last chapter, we discussed how the ventral ("what") pathway of the brain, extending from the occipital lobe into the temporal lobe, is involved in recognizing objects. One area that has been isolated within this pathway in humans is called the **lateral occipital complex (LOC)**. **Figure 5.41** shows the location of the LOC as well as a few other brain areas that we'll be discussing in this section. Research studies using brain imaging (see Method, page 31) have found that the LOC is active when the person views any kind of object—such as an animal, face, house, or tool—but not when they view a texture, or an object with the parts scrambled (Malach et al., 1995; Grill-Spector, 2003). Furthermore, the LOC is activated by objects regardless of their size, orientation, position, or other basic features.

The LOC builds upon the processing that took place in lower-level visual regions, like V1 where the neurons responded to simple lines and edges (see Chapter 4, page 69). By the time the signal proceeds up the ventral pathway and reaches the LOC, those lines have been put together into a whole object. Importantly, though, while the LOC appears to play a role in object perception, it does not differentiate between different *types* of objects, like faces versus other objects. Next, we'll discuss how more specific object categories are represented.

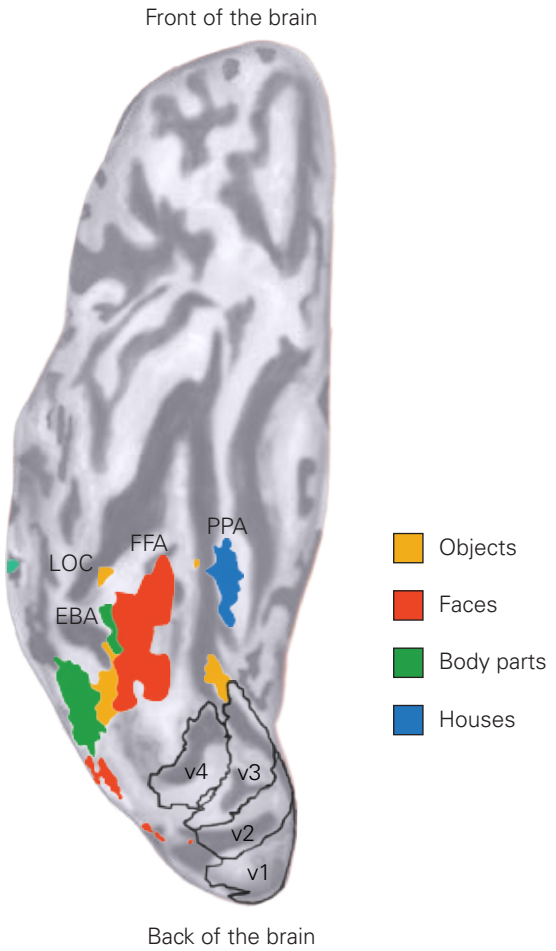

Figure 5.41 A few brain areas involved in different aspects of object and scene perception, shown here on the underside of one hemisphere of the brain. These areas are shown relative to visual areas V1–V4, which we introduced in Chapter 4 (Figure 4.23). LOC = lateral occipital complex; FFA = fusiform face area; PPA = parahippocampal place area; EBA = extrastriate body area. (From Grill-Spector, 2009)

The Neural Correlates of Face Perception In a seminal 1997 study, Nancy Kanwisher and coworkers used fMRI to determine brain activity in response to pictures of faces and other objects such as household objects, houses, and hands. When they subtracted the response to the other objects from the response to the faces, Kanwisher and coworkers found that activity remained in an area they called the **fusiform face area (FFA)**, which is located in the fusiform gyrus on the underside of the brain directly below the inferotemporal (IT) cortex introduced in Chapter 4 (Figure 5.41). This area is roughly equivalent to the face areas in the temporal cortex of the monkey. Kanwisher's results, plus the results of many

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other experiments, have suggested that the FFA is specialized to respond to faces (Kanwisher, 2010).

Additional evidence of the role of the FFA in face perception is that damage to this area can cause **prosopagnosia**—difficulty recognizing the faces of familiar people. Even very familiar faces are affected, so people with prosopagnosia may not be able to recognize close friends or family members—or even their own reflection in the mirror—although they can easily identify such people as soon as they hear them speak (Burton et al., 1991; Hecaen & Angelerques, 1962; Parkin, 1996).

So, the FFA seems to play a key role in face perception. This finding supports a modular view of neural representation, which, if you recall from Chapter 2 (p. 31), is the idea that activity in a certain brain area (or module) represents a certain function. But other research suggests that the FFA is not the only area involved in face perception. Consider, for example, that when we view a face, our experience extends beyond simply identifying it ("that's a face"). We can also respond to the following additional aspects of faces: (1) emotional aspects ("she is smiling, so she is probably happy," "looking at his face makes me happy"); (2) where someone is looking ("she's looking at me"); (3) how parts of the face move ("I can understand him better by watching his lips move"); (4) how attractive a face is ("he has a handsome face"); and (5) whether the face is familiar ("I remember her from somewhere"). Faces are complex; they cause many different reactions, and, as shown in **Figure 5.42** and **Table 5.1**, these different reactions are associated with activity in many different places in the brain—a concept consistent with a distributed view of neural representation.

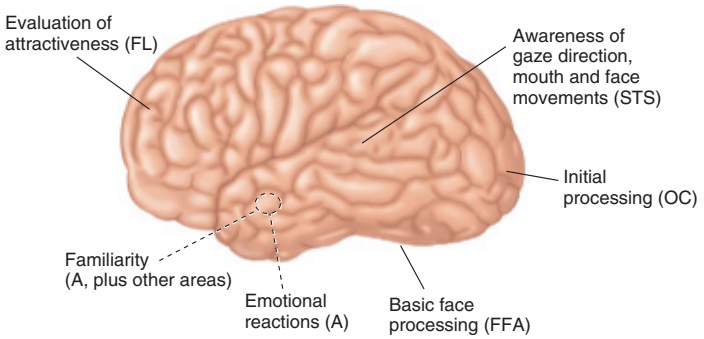
Evaluation of attractiveness (FL)
Awareness of gaze direction, mouth and face movements (STS)
Initial processing (OC)
Familiarity (A, plus other areas)
Emotional reactions (A)
Basic face processing (FFA)

Figure 5.42 Areas of the brain that are activated by different aspects of faces. OC = occipital cortex; FFA = fusiform face area; A = amygdala; FL = frontal lobe; STS = superior temporal sulcus. The dashed line for the amygdala indicates that it is located inside the brain, below the cortex.

Neural Representation of Other Categories of Objects How are other (non-face) categories of objects represented in the brain? In addition to the FFA, which contains neurons that are activated by faces, another specialized area in the temporal cortex has been identified. The **extrastriate body area (EBA)** is activated by pictures of bodies and parts of bodies, but not by faces or other objects, as shown in **Figure 5.43** (Downing et al., 2001; Grill-Spector & Weiner, 2014). Still other research suggests that categories such as animate versus inanimate objects might activate specific areas as well (Konkle & Caramazza, 2013; Martin, 2007; Martin et al., 1996).

Even though some specialized brain areas have been identified, it is unrealistic to think that we would have a distinct brain area to represent every category of object that we encounter. What's more likely is that neural representation of objects is distributed across brain areas, as we saw for faces (Figure 5.42). Evidence supporting this idea is provided by an fMRI experiment by Alex Huth and coworkers (2012) in which participants viewed 2 hours of film clips while in a brain scanner. To analyze how individual brain areas were activated by different objects and actions in the films, Huth created a list of 1,705 different objects and action categories and determined which categories were present in each film scene.

Figure 5.44 shows four movie clips and the categories (labels) associated with them. By determining how different brain areas were activated by each movie clip and then analyzing his results using a complex statistical procedure, Huth was able to determine what kinds of stimuli each brain area responded to. For example, one area responded well when streets, buildings, roads, interiors, and vehicles were present.

Figure 5.45 shows some of the categories that cause different areas across the surface of the brain to respond. Objects and actions similar to each other are located near each other in the brain. The reason there are two areas for humans and two for

Table 5.1 Brain Areas Activated by Different Aspects of Faces

AREA OF BRAIN	FUNCTION
Occipital cortex (OC)	Initial processing
Fusiform face area (FFA)	Basic face processing
Amygdala (A)	Emotional reactions (face expressions and observer's emotional reactions) Familiarity (familiar faces cause more activation in amygdala and other areas associated with emotions)
Frontal lobe (FL)	Evaluation of attractiveness
Superior temporal sulcus (STS)	Gaze direction Mouth movements General face movements

Based on Calder et al., 2007; Gobbini & Haxby, 2007; Grill-Spector et al., 2004; Ishai et al., 2004; Natu & O'Toole, 2011; Pitcher et al., 2011; Puce et al., 1998; Winston et al., 2007.

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Figure 5.43 The extrastriate body area (EBA) is activated by bodies (top), but not by other stimuli (bottom). (Kanwisher, 2003)

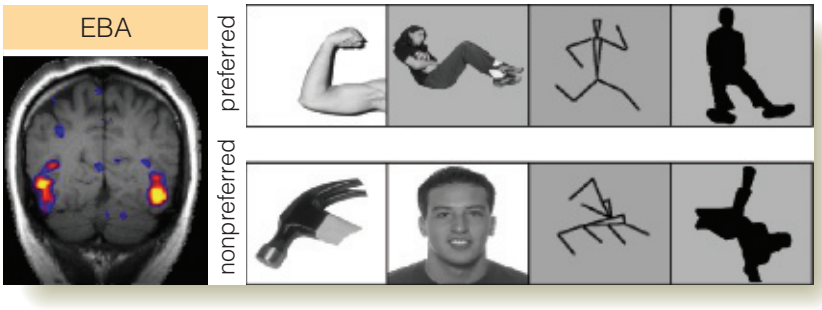

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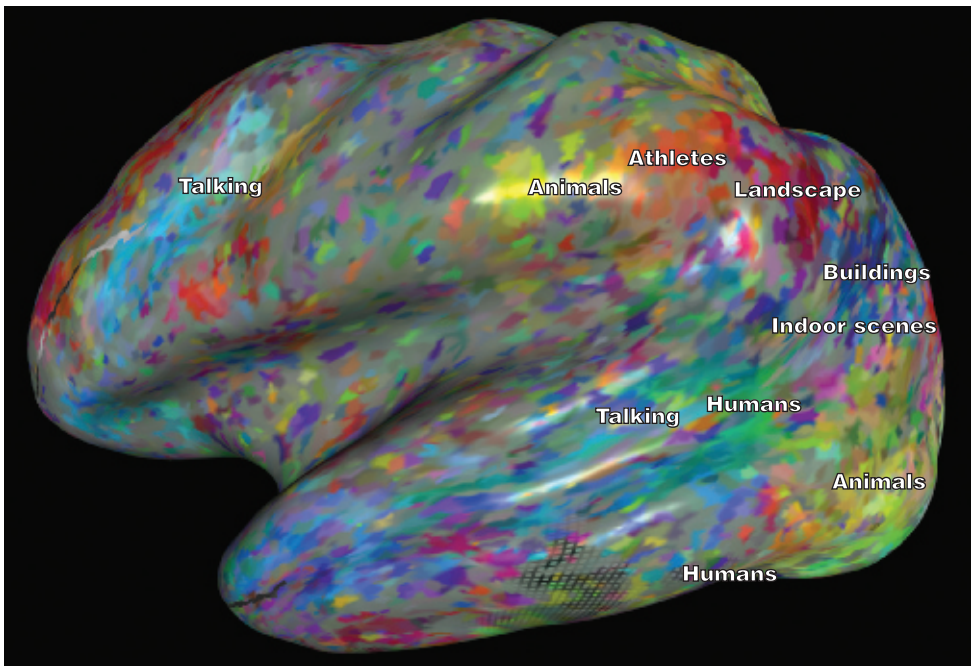
Figure 5.44 Four frames from the movies viewed by participants in Huth et al.'s (2012) experiment. The words on the right indicate categories that appear in the frames (n = noun; v = verb). (Huth et al., 2012)

Movie Clip	Labels	Movie Clip	Labels
	butte.n desert.n sky.n cloud.n brush.n		city.n expressway.n skyscraper.n traffic.n sky.n
	woman.n talk.v gesticulate.v book.n		bison.n walk.v grass.n stream.n

Figure 5.45 The results of Huth et al.'s (2012) experiment, showing locations on the brain where the indicated categories are most likely to activate the brain. Colors indicate areas that respond similarly. For example, both areas marked "Animals" are yellow. (Courtesy of Alex Huth)



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animals is that each area represents different features related to humans or animals. For example, the area labeled "human" at the bottom of the brain (which is actually on the underside of the brain) corresponds to the FFA, which responds to all aspects of faces. The human area higher on the brain responds specifically to facial expressions.

The conclusion from all this neuroimaging research is while some research suggests that there may be different modules for different functions, representation often goes beyond those modules, so that a combination of modular and distributed representation appears to underlie our perception of objects and faces.

Brain Responses to Scenes

Not long after the discovery of the role of the FFA in face perception, Russell Epstein and Nancy Kanwisher identified another specialized area in the temporal lobe—one that responds to places, but not objects or faces. They called this region the **parahippocampal place area (PPA),** which can be seen in **Figure 5.46**. Using fMRI, Epstein and Kanwisher showed that the PPA was activated by pictures depicting indoor and outdoor scenes (Aguirre et al., 1998; Epstein et al., 1999; Epstein & Kanwisher, 1998). Apparently what is important for this area is information about spatial layout, because increased activation occurs both to empty rooms and to rooms that are completely furnished (Kanwisher, 2003).

But what function does the PPA actually serve? Some researchers have asked whether the PPA really is a "place" area, as the name implies. Some of these researchers prefer the term *parahippocampal cortex (PHC)*, which identifies the location of the area in the brain without making a statement about its function.

One hypothesis for what the PPA/PHC does is Russell Epstein's (2008) **spatial layout hypothesis**, which proposes that the PPA/PHC responds to the *surface geometry* or *geometric layout* of a scene. This proposal is based partially on the fact that scenes cause larger responses than buildings. But Epstein doesn't think buildings are totally irrelevant, because the response to buildings is larger than for objects in general. Epstein explains this by stating that buildings are "partial scenes" that are associated with space, and concludes that the function of the PPA/PHC is to respond to qualities of objects that are relevant to *navigation through a scene* or *locating a place* (also see Troiani et al., 2014). When we discuss navigation through scenes in more detail in Chapter 7, we will consider more evidence linking the parahippocampal cortex to navigation and will see that other nearby brain areas are also involved in navigation.

Figure 5.46 The parahippocampal place area (PPA) is activated by places (top) but not by other stimuli (bottom). (Kanwisher, 2003)

The spatial layout hypothesis is just one proposed function of the PPA/PHC. Others have suggested that the role of the PPA/PHC is to represent three-dimensional space more generally, even if there is no scene (Mullally & Maguire, 2011). This hypothesis is based on fMRI studies showing that the PPA/PHC is activated not only by full scenes, but also by objects that create a sense of surroundings and by images that create an impression of three-dimensional space—for instance, like the foreground of the scene in Figure 5.26 (Zeidman et al., 2012). Still other researchers have proposed that the function of the PPA/PHC is to represent contextual relations—how related objects are organized in space, such as items that belong in a kitchen (Aminoff et al., 2013). Others have presented evidence that the PPA/PHC is subdivided into different areas that may have different functions, such as one subregion for the visual analysis of a scene and another subregion for connecting that visual information to a memory of the scene (Baldassano et al., 2016; Rémy et al., 2014). Although discussion of the function of the PPA/PHC is continuing among researchers, it is generally agreed that it is important for perceiving space, whether the space is defined by single objects or the more extensive areas associated with scenes.

Importantly, like we saw with the FFA and face perception, the PPA is not the only area involved in scene perception. In fact, there are at least two other areas in the occipital and temporal lobes that appear to respond selectively to scenes (Epstein & Baker, 2019), and studies assessing functional connectivity (see Methods box, page 33) have even shown that these areas are activated along with the PPA (Baldassano et al., 2016). This provides further evidence for distributed representation—that when we view a scene, multiple interconnected brain areas are involved.

The Relationship Between Perception and Brain Activity

As you walk around in your daily life, such as on campus to get to class, you likely come across many faces and buildings. However, you might not be aware that you encountered all of those faces and buildings. For instance, if you're focused on navigating to the building ahead, you might miss your friend waving at you right along the way. In this situation, is your FFA still activated in response to your friend's face? Or must you switch your perception from the building to your friend's face in order for your FFA to respond? This relationship between perception (like perceiving the face or the building) and brain activity has been explored using a technique in which different images are presented to the left and right eyes.

In normal everyday perception, our two eyes receive slightly different images because the eyes are in two slightly

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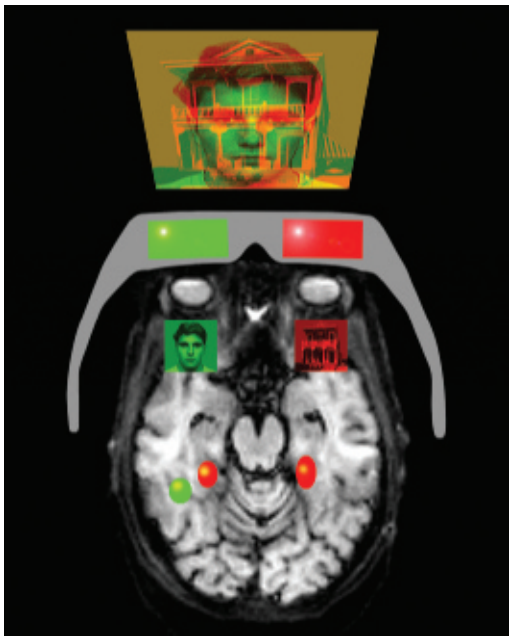

Frank Tong

Figure 5.47 Observers in Tong et al.'s (1998) experiment viewed the overlapping red house and green face through red–green glasses, so the house image was presented to the right eye and the face image to the left eye. Because of binocular rivalry, the observers' perception alternated back and forth between the face and the house. When the observers perceived the house, activity occurred in the parahippocampal place area (PPA) in the left and right hemispheres (red ellipses). When observers perceived the face, activity occurred in the fusiform face area (FFA) in the left hemisphere (green ellipse). (From Tong et al., 1998)

different locations. These two images, however, are similar enough that the brain can combine them into a single perception. But if the two eyes receive totally different images, the brain can't combine the two images and a condition called **binocular rivalry** occurs, in which the observer perceives either the left-eye image or the right-eye image, but not both at the same time.[1]

Frank Tong and coworkers (1998) used binocular rivalry to connect perception and neural responding by presenting a picture of a person's face to one eye and a picture of a house to the other eye and having observers view the pictures through colored glasses, as shown in **Figure 5.47**. The colored glasses caused the face to be presented to the left eye and the house to the right eye. Because each eye received a different image, binocular rivalry occurred, so while the images remained the same on the retina, observers perceived just the face or just the house, and these perceptions alternated back and forth every few seconds.

The participants pushed one button when they perceived the house and another button when they perceived the face, while Tong used fMRI to measure activity in the participant's PPA and FFA. When participants were perceiving the house, activity increased in the PPA (and decreased in the FFA); when they were perceiving the face, activity increased in the FFA (and decreased in the PPA). Even though the images on the retina remained the same throughout the experiment, activity in the brain changed depending on what the person was experiencing. This experiment and others like it generated a great deal of excitement among brain researchers because they measured brain activation and perception simultaneously and demonstrated a dynamic relationship between perception and brain activity in which changes in perception and changes in brain activity mirrored each other.

[1]This all-or-none effect of rivalry, in which one image is seen at a time (the house or the face), occurs most reliably when the image presented to each eye covers a small area of the visual field. When larger images are presented, observers sometimes see parts of the two images at the same time. In the experiment described here, observers generally saw either the house or the face, alternating back and forth.

Neural Mind Reading

We've presented numerous examples of experiments in which stimuli—like objects, faces, and scenes—are presented, and the brain response is measured. Some researchers have reversed the process, measuring the person's brain response and determining the stimuli that generated that response. They achieve this using a procedure we will call *neural mind reading*.

METHOD | Neural Mind Reading

Neural mind reading refers to using a neural response, usually brain activation measured by fMRI, to determine what a person is perceiving or thinking. As we saw in Chapter 2 (page 31), fMRI measures the activity in *voxels*, which are small cube-shaped volumes in the brain about 2 or 3 mm on a side. In neural mind reading, what's important is the *pattern* of activation across multiple voxels, which is often measured using a technique called multivoxel pattern analysis (MVPA). The pattern of voxels activated depends on the task and the nature of the stimulus being perceived. For example, **Figure 5.48a** shows eight voxels that are activated by a black-and-white grating stimulus slanted to the right. Viewing a different orientation (for instance, slanted to the left) activates a different pattern of voxels.

Figure 5.49 illustrates the basic procedure for neural mind reading using these oriented gratings as an example (Kamitani & Tong, 2005). First, the relationship between the stimulus and the voxel pattern is determined by measuring the brain's response to a number of different stimuli (in this case, different orientations) using fMRI (**Figure 5.49a**). We'll call this the calibration phase. Then, these data are used to create a decoder, which is a computer program that can predict the most likely stimulus based on the voxel activation patterns observed in the calibration phase (**Figure 5.49b**). Finally, in the testing phase, the performance of the decoder is tested by measuring brain activation as a person is looking at different stimuli, as before, but this time using the decoder to predict the stimulus the person is perceiving (**Figure 5.49c**). If this works, it should be possible to predict what stimulus a person is looking at based on his or her brain activation alone.

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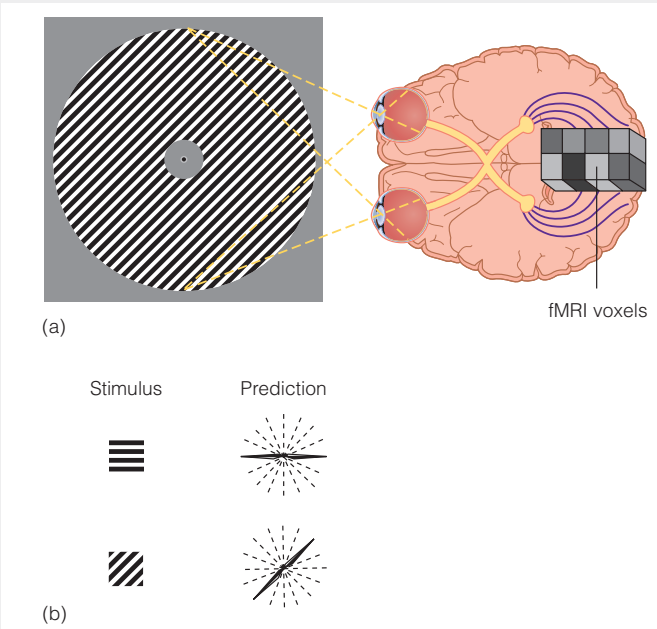

Figure 5.48 (a) Viewing an oriented grating like the one on the left causes a pattern of activation of voxels. The cubes in the brain represent the response of eight voxels. The differences in shading represent the pattern of activation of the orientation being viewed. (b) Results of Kamitani and Tong's (2005) experiment for two orientations. The gratings are the stimuli presented to the observer. The line is the orientation predicted by the decoder. The decoder was able to accurately predict the orientations of all eight of the gratings tested. (From Kamitani & Tong, 2005)

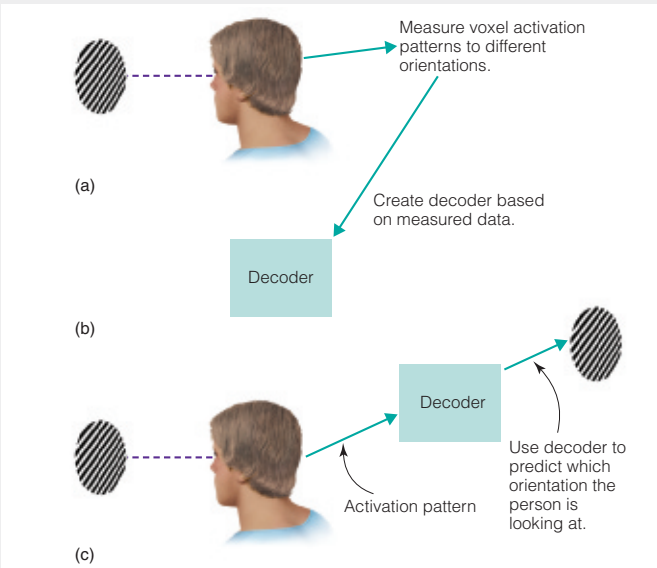

Figure 5.49 Principle behind neural mind reading. (a) In the calibration phase, the participant looks at different orientations, and fMRI is used to determine voxel activation patterns for each orientation. (b) A decoder is created based on the voxel patterns collected in (a). (c) In the testing phase, a participant looks at an orientation, and the decoder analyzes the voxel pattern recorded from the participant's visual cortex. Based on this voxel pattern, the decoder predicts the orientation that the participant is observing.

When Yukiyasu Kamitani and Frank Tong (2005) used the procedure above, they were able to predict, based on the pattern of activity of 400 voxels in the visual cortex, the orientations of eight different gratings that a person was observing (**Figure 5.48b**).

Creating a decoder that can determine from brain activity what orientation a person is perceiving was an impressive achievement. But what about complex stimuli like objects and scenes? Expanding our stimulus set from eight grating orientations to every possible object and scene in the environment is quite a jump! But amazingly, recent work toward creating such complex decoders has had some success.

One such study was conducted by Shinji Nishimoto and coworkers (2011), whose goal was to see if they could make a decoder that was able to reconstruct, or recreate, what the participant was seeing in a movie using just their brain activation. First, in the calibration phase, they showed participants over 7,000 seconds of movie clips in the fMRI scanner while recording the patterns of voxel activation in the visual cortex. The decoder was given these voxel activation patterns and trained to learn how the participant's brain typically responds to different visual stimuli. As one of the authors on this study, Jack Gallant, once described, it's almost like the computer is building a "dictionary" that translates between the stimuli in the movie clips and the participant's brain responses to those stimuli (Ross, 2011).

Then in the testing phase, the participants saw new movie clips that they had not seen during the calibration phase. The goal was to determine whether the decoder could use "dictionary"—the participant's activation patterns acquired during the calibration phase—to predict what they were seeing on a second-by-second basis in these new movie clips. In other words, the decoder would read the brain activation pattern acquired during the testing phase, and then "look up" that pattern in the dictionary that it created during the calibration phase in order to predict what stimulus the person was seeing.

The interesting part about this study was that not only could the decoder look up the stimulus that most closely matched the brain activation (say, that the participant was viewing a "person"), it could also create a reconstruction of what that stimulus might have looked like (the "person" was on the left side of the screen and had dark hair). To make this reconstruction, the decoder consulted a database of 18 million seconds of movie clips collected from the Internet (clips not used during calibration or testing) and was programmed to pick the clips that most closely matched the stimulus that it had "looked up" in the brain activation pattern dictionary (i.e., clips showing a person on the left side of the screen with dark hair). The decoder then took an average of all of those matching clips to produce a visual reconstruction, or a "best guess," of what the participant was most likely seeing during each second of the movie. Altogether, an astounding computational feat!

So, could the decoder actually read participants' minds and guess what they were seeing in the movie clips during the testing phase? The left column in **Figure 5.50** shows images from film clips that the participant observed. The right column

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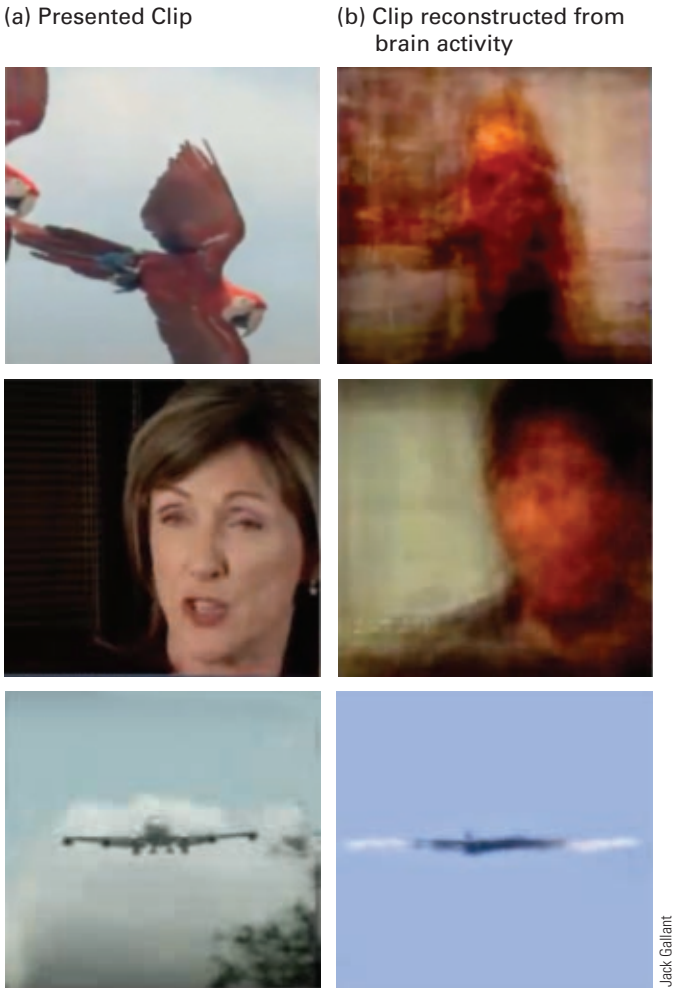

Figure 5.50 Results of a neural mind reading experiment. Left column: Images from film clips. Right column: Image created by the computer. (Nishimoto et al., 2011)

shows the computer's best guess of what the participant was seeing, based on their brain activation. Although some fine detail is missing, you can see that overall, the decoder did a pretty good job! It could determine that the participant was looking at a face, for instance, versus some abstract shape.

Nishimoto and coworkers' study provides some strong evidence that neural mind reading is becoming possible, and other recent studies continue to confirm this in vision and even in other senses, like hearing (Formisano et al., 2008; Huth et al., 2016). What's still limiting about the current mind reading methods is that there needs to be a "calibration" phase; in other words, researchers first need to present the stimulus to determine the brain activation pattern in order to use the brain activation pattern to determine the stimulus. So, it's not that decoders can just read anyone's mind; they need to first see how someone's brain responds to certain inputs. This means that the stimuli that the researchers choose as the inputs (and potential outputs) is also limiting. Eventually, though, much larger image databases will result in matches that are much closer to the target. Accuracy will also increase as we learn more about how the neural activity of various areas of the brain represents the characteristics of objects and scenes.

Of course, the ultimate decoder won't need a calibration phase or to compare its output to huge image databases. It will just analyze the voxel activation patterns and recreate the image of the scene. Presently, there is only one "decoder" that has achieved this, and that is your own brain! Although it is worth noting that your brain does make use of a "database" of information about the environment, as we know from the role of regularities of the environment in perceiving scenes. This ultimate decoder is still far from being achieved in the laboratory. However, the decoders that presently exist are amazing achievements, which only recently might have been classified as "science fiction."

SOMETHING TO CONSIDER:

The Puzzle of Faces

Having described perceptual organization and how we perceive objects and scenes, we now focus again on one specific type of object: faces. We focus on faces because faces are pervasive in the environment, and they are important sources of information. Faces establish a person's identity, which is important for social interactions (who is the person who just said hello to me?) and for security surveillance (checking people as they pass through airport security). Faces also provide information about a person's mood and where the person is looking, and can elicit evaluative judgments (the person seems unfriendly, the person is attractive, and so on).

Faces have also been the topic of a great deal of research. Some of this research argues that there is something special about faces. For example, when people are asked to look as rapidly as possible at a picture of either a face, an animal, or a vehicle, faces elicit the fastest eye movements, occurring within 138 ms, compared to 170 ms for animals and 188 ms for vehicles (Crouzet et al., 2010). Results such as these have led to the suggestion that faces have special status that allows them to be processed more efficiently and faster than other classes of objects (Crouzet et al., 2010; Farah et al., 1998).

One research finding that had been repeated many times is that inverting a picture of a face (turning it upside down) makes it more difficult to identify the face or to tell if two inverted faces are the same or different (Busigny & Rossion, 2010). Similar effects occur for other objects, such as cars, but the effect is much smaller (**Figure 5.51**).

Because inverting a face makes it more difficult to process configurational information—the relationship between features such as the eyes, nose, and mouth—the inversion effect has been interpreted as providing evidence that faces are processed

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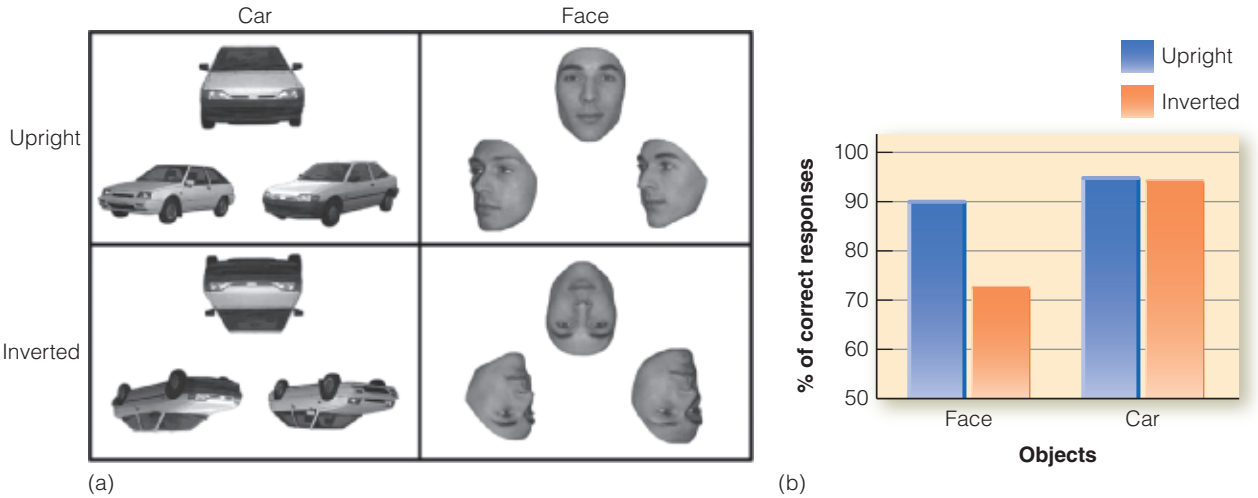

Figure 5.51 (a) Stimuli from Busigny and Rossion's (2010) experiment in which participants were presented with a front view of a car or a face and were asked to pick the three-quarter view that was the same car or face. For example, the car on the right in the upper panel is the same car as the one shown in front-view above. (b) Performance for upright cars and faces (blue bars) and inverted cars and faces (orange bars). Notice that inverting the cars has little or no effect on performance but that inverting faces causes performance to decrease from 89 percent to 73 percent. (From Busigny & Rossion, 2010)

holistically (Freire et al., 2000). Thus, while all faces contain the same basic features—two eyes, a nose, and a mouth—our ability to distinguish thousands of different faces seems to be based on our ability to detect the configuration of these features—how they are arranged relative to each other on the face. This research suggests that faces are special because they are processed differently (more holistically) than other objects.

Faces may also be special because, as we've discussed in this and previous chapters, there are neurons that respond selectively to faces, and there are specialized places in the brain that are rich in these neurons. One such area, which we described earlier in this chapter, is the area in the fusiform gyrus that Nancy Kanwisher dubbed the *fusiform face area (FFA)*, because it seemed to respond selectively to faces (Kanwisher et al., 1997). As it turns out, however, later research has shown that there are neurons in the FFA that respond to objects other than faces (Haxby et al., 2001), but the name *fusiform face area* has stuck, and it is likely that even if the FFA may not respond exclusively to faces, it plays an important role in face perception.

Of course, there's more to the physiology of face perception than the FFA; as we saw when we described the neural correlates of face perception on page 110, numerous areas in addition to the FFA are involved in face perception (see Figure 5.42).

Faces are therefore special both because of the role they play in our environment and because of the widespread activity they trigger in the brain.

But we're not finished with faces yet, because faces have been at the center of one of the more interesting controversies in perception, which involves the **expertise hypothesis**, the idea that our proficiency in perceiving faces, and the large face response in the FFA, can be explained by the fact that we have become "experts" in perceiving faces because we've been exposed to them for our entire lives.

In support of the expertise hypothesis, Isabel Gauthier and coworkers (1999) used fMRI to determine the FFA response to faces and to objects called "Greebles"—families of computer-generated "beings" that all have the same basic configuration but differ in the shapes of their parts (**Figure 5.52a**). Initially, the participants were shown both human faces and Greebles. The results for this part of the experiment, shown by the left pair of bars in **Figure 5.52b**, indicate that the FFA neurons responded poorly to the Greebles but well to the faces.

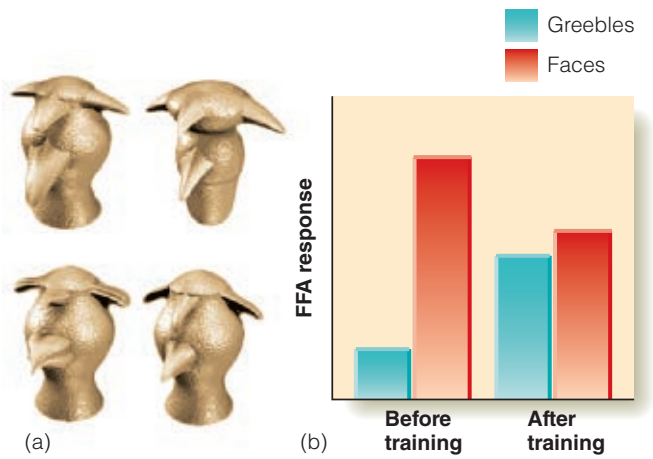

Figure 5.52 (a) Greeble stimuli used by Gauthier. Participants were trained to name each different Greeble. (b) Brain responses to Greebles and faces before and after Greeble training. (From Gauthier et al., 1999)

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The participants were then trained in "Greeble recognition" for 7 hours over a 4-day period. After the training sessions, participants had become "Greeble experts," as indicated by their ability to rapidly identify many different Greebles by the names they had learned during the training. The right pair of bars in Figure 5.52b shows that after the training, the FFA responded about as well to Greebles as to faces.

Based on this result, Gauthier suggested that the FFA might not be a "face area" after all, but may instead represent any object with which the person is an expert (which happens to include faces). In fact, Gauthier has also shown that the FFA of people who are experts in recognizing cars or birds responds well not only to human faces but to cars (for the car experts) and to birds (for the bird experts; Gauthier et al., 2000). Similarly, another study showed that viewing the positions of chess pieces on a chess board causes a larger activation of the FFA in chess experts than in nonexperts (Bilalić et al., 2011).

What does all this mean? All we can say for sure is that the question of whether faces are inherently special, or whether their "specialness" is simply due to our extensive experience with them, is still controversial. Some researchers agree that experience is important for establishing the FFA as a module for faces (Bukach et al., 2006; Tanaka & Curran, 2001); others argue that the FFA's role as a face area is based largely on built-in wiring that doesn't depend on experience (Kanwisher, 2010). This debate about face specificity and the FFA demonstrates that even with all of the research on face and object perception that has occurred over the past 30 years, controversies and uncertainties still exist.

DEVELOPMENTAL DIMENSION Infant Face Perception

What do newborns and young infants see? In the Developmental Dimension in Chapter 3 (p. 60), we saw that infants have poor detail vision compared to adults but that the ability to see details increases rapidly over the first year of life. We should not conclude from young infants' poor detail vision, however, that they can see nothing at all. At very close distances, a young infant can detect some gross features, as indicated in **Figure 5.53**, which simulates how infants perceive a face from a distance of about 2 feet. At birth, the contrast perceived between light and dark areas is so low that it is difficult to determine it is a face, but it is possible to see very high contrast areas. By 8 weeks, however, the infant's ability to perceive the contrast between light and dark perception has improved so that the image looks clearly facelike. By 3 to 4 months, infants can tell the difference between faces that look happy and those that show surprise, anger, or are neutral (LaBarbera et al., 1976; Young-Browne et al., 1977) and can also tell the difference between a cat and a dog (Eimas & Quinn, 1994).

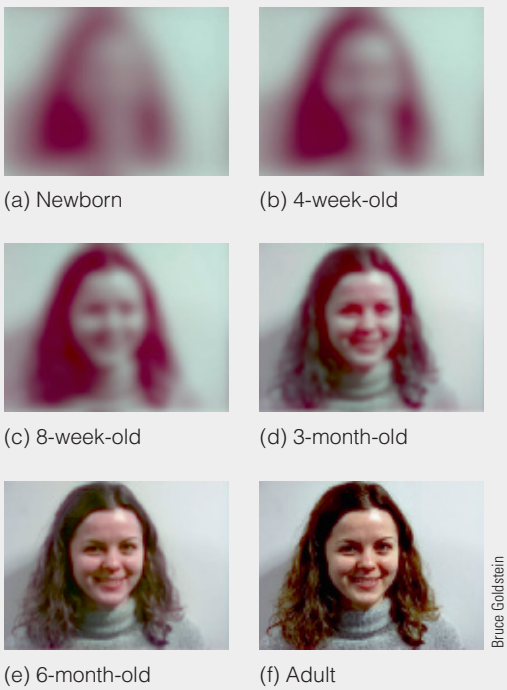

Figure 5.53 Simulations of perceptions of a mother located 124 inches from an observer, as seen by newborns and various ages. (Simulations courtesy of Alex Wade)

Human faces are among the most important stimuli in an infant's environment. As a newborn or young infant stares up from the crib, numerous faces of interested adults appear in the infant's field of view. The face that the infant sees most frequently is usually the mother's, and there is evidence that young infants can recognize their mother's face shortly after they are born.

Using preferential looking in which 2-day-old infants were given a choice between their mother's face and a stranger's, Ian Bushnell and coworkers (1989) found that newborns looked at the mother's face about 63 percent of the time. This result is above the 50 percent chance level, so Bushnell concluded that the 2-day-olds could recognize their mother's face.

To determine what information the infants might be using to recognize the mother's face, Olivier Pascalis and coworkers (1995) showed that when the mother and the stranger wore pink scarves that covered their hairline, the preference for the mother disappeared. The high-contrast border between the mother's dark hairline and light forehead apparently provides important information about the mother's physical characteristics that infants use to recognize the mother (see Bartrip et al., 2001, for another experiment that shows this).

In an experiment that tested newborns within an hour after they were born, John Morton and Mark Johnson (1991) presented stimuli (see bottom of **Figure 5.54**) to the newborns and then moved the stimuli to the left and right. As they did this, they videotaped the infant's face. Later, scorers who were

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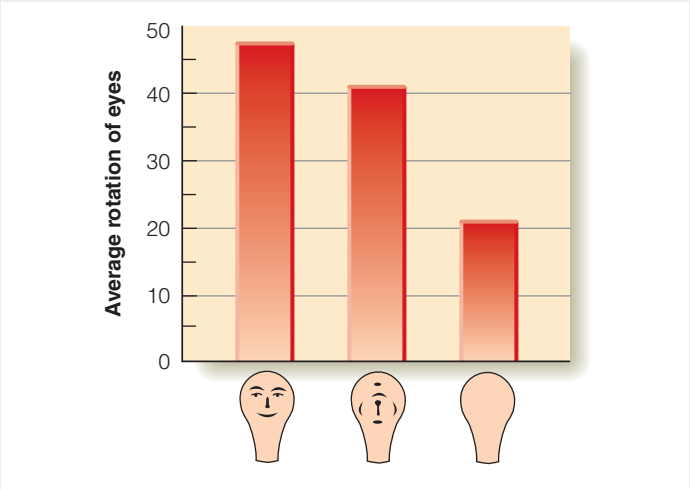

Figure 5.54 The magnitude of infants' eye movements in response to movement of each stimulus. The average rotation of the infants' eyes was greater for the facelike stimulus than for the scrambled-face stimulus or the blank stimulus. (Adapted from Morton & Johnson, 1991)

unaware of which stimulus had been presented viewed the tapes and noted whether the infant turned its head or eyes to follow the moving stimulus. The results in the graph in Figure 5.54 show that the newborns looked at the moving face more than at the other moving stimuli, which led Morton and Johnson to propose that infants are born with some information about the structure of faces. In support of this proposal, a neuroimaging study by Teresa Farroni and coworkers (2013) found that in 1- to 5-day old newborns, moving face stimuli—such as a video of an adult playing the game "peek-a-boo"—elicited more activity in visual brain areas than moving non-face stimuli, such as a video of cogs and pistons. This neuroimaging study adds to the behavioral evidence suggesting an innate predisposition for perceiving faces.

But there is also evidence for a role of experience in infant face perception. Ian Bushnell (2001) observed newborns over the first 3 days of life to determine whether there was a relationship between their looking behavior and the amount of time they were with their mother. He found that at 3 days of age, when the infants were given a choice between looking at a stranger's face or their mother's face, the infants who had been exposed to their mother longer were more likely to prefer her over the stranger. The two infants with the lowest exposure to the mother (an average of 1.5 hours) divided their looking evenly between the mother and stranger, but the two infants with the longest exposure (an average of 7.5 hours) looked at the mother 68 percent of the time. Analyzing the results from all of the infants led Bushnell to conclude that face perception emerges very rapidly after birth, but that experience in looking at faces does have an effect.

Although the infant's ability to recognize faces develops rapidly over the first few months, these impressive gains are only a starting point, because even though 3- to 4-month-old infants can recognize some facial expressions, their ability to identify faces doesn't reach adult levels until adolescence or early adulthood (Grill-Spector et al., 2008; Mondloch et al., 2003, 2004).

What about physiology? A recent study measured functional connectivity in the brains of infants who were 27 days old. Functional connectivity occurs when the neural activity in two different areas of the brain is correlated (see page 34). Frederik Kamps and coworkers (2020) measured functional connectivity in sleeping infants using the resting state fMRI method (see Method, Chapter 2, page 34) and identified a functional connection between the visual cortex, where information about faces first reaches the cortex, and the fusiform face area—two areas that are not yet well developed in infants, but that are associated with face perception in adults.

Kamps concludes from this result that "connectivity precedes function" in the developing cortex. According to this idea, the connection between the visual cortex and what will become the FFA is prewired, setting the stage for further development of the infant's face perception abilities.

But the development of the physiology of face perception stretches out over many years. **Figure 5.55** shows that the FFA, indicated by red, is small in an 8-year-old child compared to the FFA in an adult (Golarai et al., 2007; Grill-Spector et al., 2008). In contrast, the PPA, indicated by green, is similar in the 8-year-old child and the adult.

It has been suggested that this slow development of the specialized face area may be related to the maturation of the ability to recognize faces and their emotions, and especially the ability to perceive the overall configuration of facial features (Scherf et al., 2007). Thus, the specialness of faces extends from birth, when newborns can react to some aspects of faces, to late adolescence, when the true complexity of our responses to faces finally emerges.

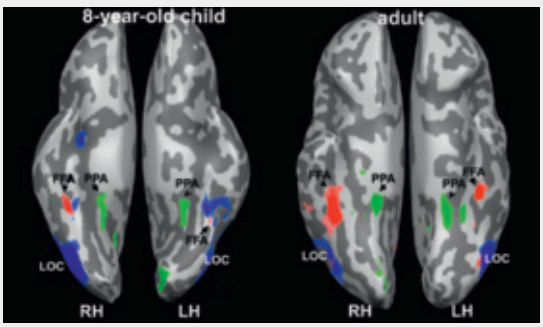

Figure 5.55 Face (red), place (green), and object (blue) selective activations for one representative 8-year-old and one representative adult. The place and object areas are well developed in the child, but the face area is small compared to the adult. (From Grill-Spector et al., 2008)

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TEST YOURSELF 5.3

1. What is the role of the lateral occipital complex in perception?
2. Describe the evidence suggesting that the FFA is involved in perceiving faces. Be sure your answer includes a description of prosopagnosia.
3. Discuss how other (non-face) categories of objects are represented in the brain, including the fMRI study by Huth and coworkers. What does this say about modular versus distributed representation?
4. What is the role of the PPA/PHC in scene perception? Describe the function of the PPA/PHC according to the spatial layout hypothesis. What are some other proposed functions of this area?
5. Describe Tong's experiment in which he presented a picture of a house to one eye and a picture of a face to the other eye. What did the results indicate?
6. What is multivoxel pattern analysis? Describe how "decoders" have enabled researchers to use the brain's response, measured using fMRI, to predict what a person is seeing.
7. Describe two experiments showing that neural mind reading is possible. What are some limitations of these experiments?
8. Why do some researchers believe that faces are "special"? What do the eye movement experiments and the face inversion experiments show?
9. What are some areas in addition to the fusiform face area that are involved in perceiving faces?
10. What is the expertise hypothesis? Describe the fMRI evidence supporting this idea. Describe the experiment which studied faces by measuring functional connectivity.
11. What is the evidence that newborns and young infants can perceive faces? What is the evidence that perceiving the full complexity of faces does not occur until late adolescence or adulthood?

THINK ABOUT IT

1. Reacting to the announcement of the Google driverless car, Harry says, "Well, we've finally shown that computers can perceive as well as people." How would you respond to this statement?
2. Vecera showed that regions in the lower part of a stimulus are more likely to be perceived as figure (p. 120). How does this result relate to the idea that our visual system is tuned to regularities in the environment?
3. When you first look at **Figure 5.56**, do you notice anything funny about the walkers' legs? Do they initially appear tangled? What is it about this picture that makes the legs appear to be perceptually organized in that way? Can you relate your perception to any of the laws of perceptual organization? To cognitive processes based on assumptions or past experience? (pp. 96, 105)
4. Continued research on neural mind reading has explored potential applications of decoding one's neural activity. For instance, MVPA has been shown to be able to determine whether someone is telling the truth or lying, just based on their typical pattern of brain activation associated with each (Davatzikos et al., 2005; Jiang et al., 2015). Can you think of any other real-world applications of neural mind reading? What (if any) are the ethical implications of this intriguing technique?

Charles Feil

Figure 5.56 Is there something wrong with these people's legs? (Or is it just a problem in perception?)

Answers for Figure 5.7

Will Smith, Taylor Swift, Barak Obama, Hillary Clinton, Jackie Chan, Ben Affleck, Oprah Winfrey

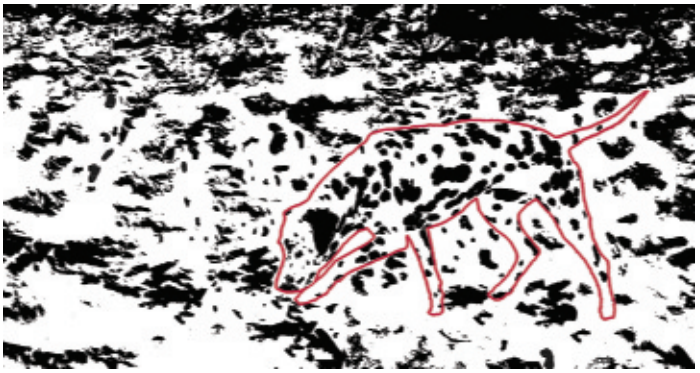

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Figure 5.57 The Dalmatian in Figure 5.10.

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KEY TERMS

Apparent movement (p. 95)
Bayesian inference (p. 108)
Binocular rivalry (p. 114)
Border ownership (p. 100)
Decoder (p. 114)
Expertise hypothesis (p. 117)
Extrastriate body area (EBA) (p. 111)
Figural cues (p. 100)
Figure (p. 99)
Figure–ground segregation (p. 99)
Fusiform face area (FFA) (p. 110)
Geons (p. 102)
Gestalt psychologist (p. 94)
Gist of a scene (p. 103)
Global image features (p. 104)
Ground (p. 99)
Grouping (p. 94)
Illusory contour (p. 96)
Inverse projection problem (p. 92)
Lateral occipital complex (LOC) (p. 110)
Light-from-above assumption (p. 105)
Likelihood (p. 108)
Likelihood principle (Helmholtz) (p. 108)
Multivoxel pattern analysis (MVPA) (p. 114)
Neural mind reading (p. 114)
Object recognition (p. 90)
Parahippocampal place area (PPA) (p. 113)
Perceptual organization (p. 94)
Persistence of vision (p. 104)
Physical regularities (p. 105)
Pragnanz (p. 97)
Prediction (p. 108)
Predictive coding (p. 109)
Principle of common fate (p. 98)
Principle of common region (p. 98)
Principle of good continuation (p. 96)
Principle of good figure (p. 97)
Principle of pragnanz (p. 97)
Principle of proximity (nearness) (p. 98)
Principle of similarity (p. 98)
Principle of simplicity (p. 97)
Principle of uniform connectedness (p. 98)
Principles of perceptual organization (p. 96)
Prior (p. 108)
Prior probability (p. 108)
Prosopagnosia (p. 111)
Recognition by components (RBC) theory (p. 102)
Regularities in the environment (p. 105)
Reversible figure–ground (p. 99)
Scene (p. 103)
Scene schema (p. 106)
Segregation (p. 94)
Semantic regularities (p. 106)
Spatial layout hypothesis (p. 113)
Structuralism (p. 94)
Unconscious inference (p. 108)
Viewpoint invariance (p. 94)
Visual masking stimulus (p. 104)

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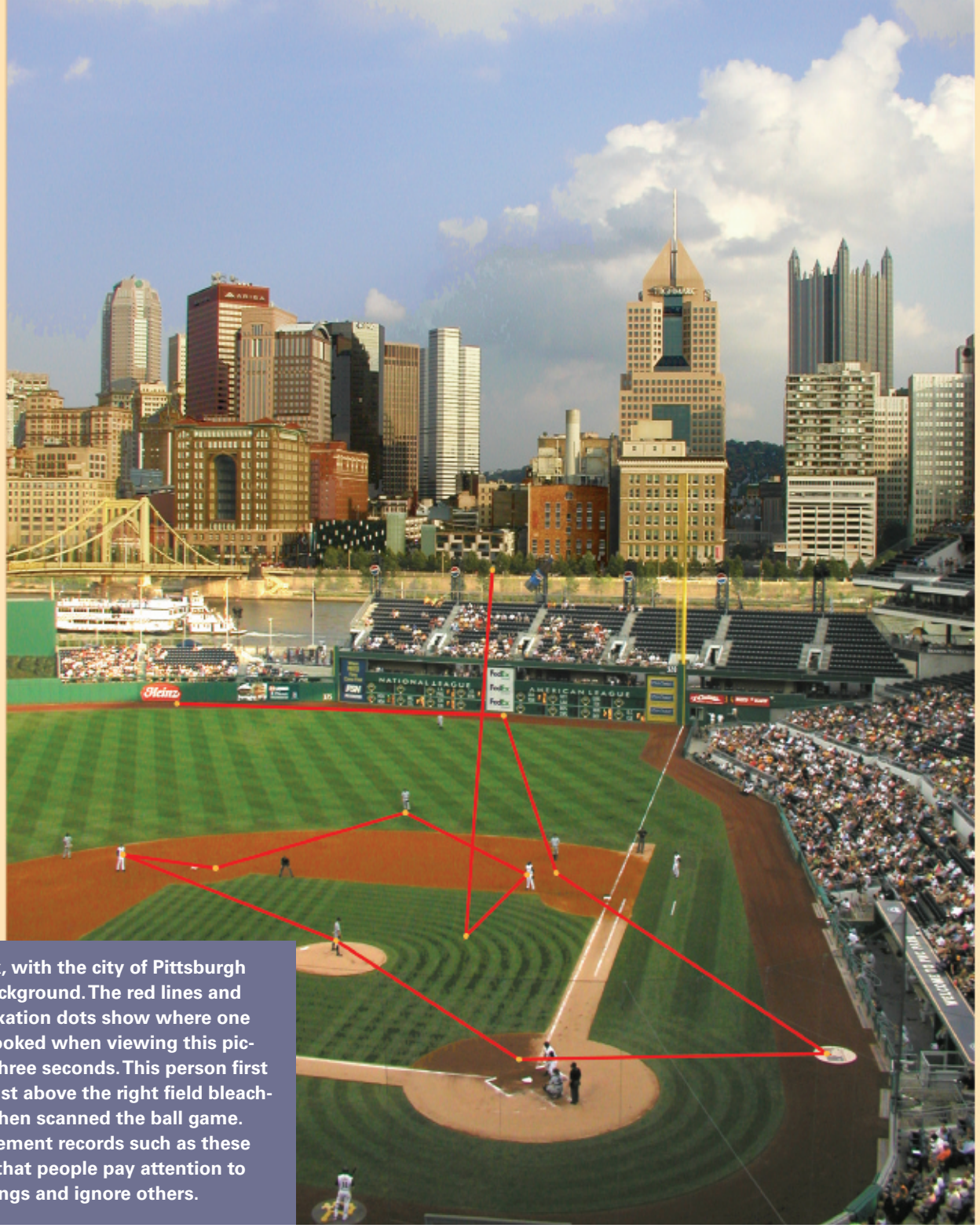

PNC Park, with the city of Pittsburgh in the background. The red lines and yellow fixation dots show where one person looked when viewing this picture for three seconds. This person first looked just above the right field bleachers and then scanned the ball game. Eye movement records such as these indicate that people pay attention to some things and ignore others.

Photo by Bruce Goldstein; Eye movement record courtesy of John Henderson

Learning Objectives

After studying this chapter, you will be able to …

- Describe early attention experiments using the techniques of dichotic listening, precueing, and visual search.
- Describe how we scan a scene by moving our eyes, and why these eye movements don't cause us to perceive the scene as smeared.
- Describe four different factors that determine where we look and the experiments that support each factor.
- Describe how attention affects physiological responding.
- Understand what happens when we don't attend and when distraction disrupts attention.
- Describe how disorders of attention teach us about basic mechanisms of attention.
- Understand the connection between meditation, attention, and mind-wandering.
- Describe how head-mounted eye tracking has been used to study how infants learn the names of objects.

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CHAPTER 6

Visual Attention

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DEVELOPMENTAL DIMENSION: Infant Attention and Learning Object Names

METHOD: Head-Mounted Eye Tracking

TEST YOURSELF 6.2

THINK ABOUT IT

Some Questions We Will Consider:

- Why do we pay attention to some parts of a scene but not to others? (p. 130)
- Does paying attention to an object make the object "stand out"? (p. 134)
- How does distraction affect driving? (p. 138)
- How does damage to the brain affect where a person attends to in space? (p. 141)

In Chapter 5 we saw that our perception of objects and scenes can't be explained by considering only the image on the retina. Although the image on the retina is important, we also need to consider explanations, such as Helmholtz's unconscious inference and predictive coding, that involve mental processing to understand how the information provided by the image on the retina becomes transformed into perception.

The idea that mental processing plays an important role in determining our perceptions is a story that continues throughout this book. This chapter continues this story by describing how we pay attention to certain things and ignore others, and what that means for visual processing.

The idea of paying attention to some things while ignoring others was described in the 19th century by William James (1842–1910), the first professor of psychology at Harvard. James relied not on the results of experiments but rather on his own personal observations when making statements such

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as the following description of attention, from his 1890 textbook *Principles of Psychology*:

> Millions of items ... are present to my senses which never properly enter my experience. Why? Because they have no interest for me. My experience is what I agree to attend to ... Everyone knows what attention is. It is the taking possession by the mind, in clear and vivid form, of one out of what seem several simultaneously possible objects or trains of thought ... It implies withdrawal from some things in order to deal effectively with others.

Thus, according to James, we focus on some things to the exclusion of others. As you walk down the street, the things you pay attention to—a classmate you recognize, the "Don't Walk" sign at a busy intersection, the fact that just about everyone except you seems to be carrying an umbrella—stand out more than many other things in the environment. The reason you are paying attention to those things is that saying hello to your friend, not crossing the street against the light, and your concern that it might rain later in the day are all important to you.

But there is also another reason for paying attention to some things and ignoring others. Your perceptual system has a limited capacity for processing information (Carrasco, 2011; Chun et al., 2011). Thus, to prevent overloading the system and therefore not processing anything well, the visual system, in James's words, "withdraws from some things in order to deal more effectively with others."

6.1 What Is Attention?

Attention is the process which results in certain sensory information being selectively processed over other information. The key words in the definition above are *selectively processed*, because they mean that something special is happening to whatever is being attended.

This definition, while correct, does not capture the wide range of things we attend to, such as a specific object (a football player running down the field; a building on campus), a particular place (a location where someone is supposed to meet you; the projection screen at the front of a classroom), a specific sound (a conversation at a party; a siren in the street), or a particular stream of thought ("what am I going to do tonight?" "What is the solution to this math problem?").

In addition to attending to different types of things, we can attend in different ways. One way of paying attention, called **overt attention**, occurs when you move your eyes from one place to another, to focus on a particular object or location. Another way of paying attention, called **covert attention**, occurs when you shift attention without moving your eyes, as might occur when you are looking at the person you are talking to but are keeping track of another person who is off to the side.

6.2 The Diversity of Attention Research

Continuing with the idea that we direct our attention to different things and in different ways, we will now describe three different approaches to attention. These approaches both illustrate the diversity of attention research, and provide examples of classic experiments from the early history of modern attention research, which began in the 1950s.

Attention to an Auditory Message: Cherry and Broadbent's Selective Listening Experiments

One of the first modern attention experiments involved hearing. Colin Cherry (1953) used a technique called **dichotic listening**, where *dichotic* refers to presenting different stimuli to the left and right ears. Cherry's experiment involved **selective attention**, because the participant's task was to selectively focus on the message in one ear, called the attended ear, and to repeat what he or she is hearing out loud. This procedure of repeating the words as they are heard is called **shadowing** (**Figure 6.1**).

Cherry found that although his participants could easily shadow a spoken message presented to the attended ear, and they could report whether the unattended message was male or female, they couldn't report what was being said in the unattended ear. Other dichotic listening experiments confirmed that people are not aware of the information being presented to the unattended ear. For example, Neville Moray (1959) showed that participants were unaware of a word that had been repeated 35 times in the unattended ear. The ability to focus on one stimulus while filtering out other stimuli is called the **cocktail party effect**, because at noisy parties people are able to focus on what one person is saying even though there are many conversations happening at the same time.

Figure 6.1 In the shadowing procedure, which involves dichotic listening, a person repeats out loud the words in the attended message as they hear them. This ensures that participants are focusing their attention on the attended message.

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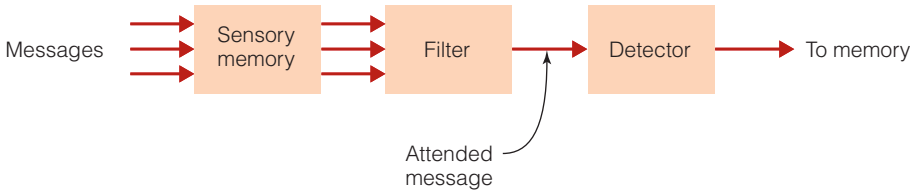

Figure 6.2 Flow diagram of Broadbent's filter model of attention.

Based on results such as these, Donald Broadbent (1958) created a model of attention designed to explain how it is possible to focus on one message and why information isn't taken in from other messages. The model proposed something that was revolutionary in the psychology of the 1950s—a flow diagram that pictured attention as a sequence of steps. This flow diagram provided researchers with a way of thinking about attention in terms of processing information, much like computer flow diagrams that were being introduced at that time.

Broadbent's flow diagram, shown in **Figure 6.2**, shows a number of messages entering a filter unit, which lets through the attended message, and filters out all of the other messages. The attended message is then detected by the detector unit and is perceived. We won't go into the details of Broadbent's model here. Its main importance is that it provides a mechanism by which attention makes the attended stimulus available for more processing. As we will see next, Michael Posner took another approach, which highlighted the effect of attention on processing.

Attention to a Location in Space: Michael Posner's Precueing Experiment

We often pay attention to specific locations, as when paying attention to what is happening in the road directly in front of our car when driving. Paying attention informs us about what is happening at a location, and also enables us to respond more rapidly to anything that happens in that location.

Attention to a specific location is called **spatial attention**. In a classic series of studies on spatial attention, Michael Posner and coworkers (1978) asked whether paying covert attention to a location improves a person's ability to respond to stimuli presented there. To answer this question, Posner used the **precueing** procedure.

METHOD | Precueing

The general principle behind a precueing experiment is to determine whether presenting a cue indicating where a test stimulus will appear enhances the processing of the test stimulus. The participants in Posner and coworkers' (1978) experiment kept their eyes stationary throughout the experiment, always looking at the + in the display in **Figure 6.3**. They first saw an arrow cue (as shown in the left panel) indicating on which side of the target a stimulus was likely to appear. In **Figure 6.3a**, the arrow cue indicates that participants should focus their attention to the right. (Remember, they do this without moving their eyes, so this is an example of covert attention.) The participants' task was to press a key as rapidly as possible when a target square was presented off to the side (as shown in the right panel). The trial shown in Figure 6.3a is a *valid trial* because the square appears on the side indicated by the cue arrow. The location indicated by the cue arrow was valid 80 percent of the time, but 20 percent of the trials were invalid; that is, the arrow cue indicated that the target was going to be presented on one side but it actually appeared on the other side, as shown in **Figure 6.3b**. For this *invalid trial*, the arrow cue indicates that the participant should attend to the left, but the target is presented on the right.

The results of this experiment, shown in **Figure 6.3c**, indicate that participants reacted more rapidly in a detection task on valid trials than on invalid trials. Posner interpreted this result as showing that information processing is more effective

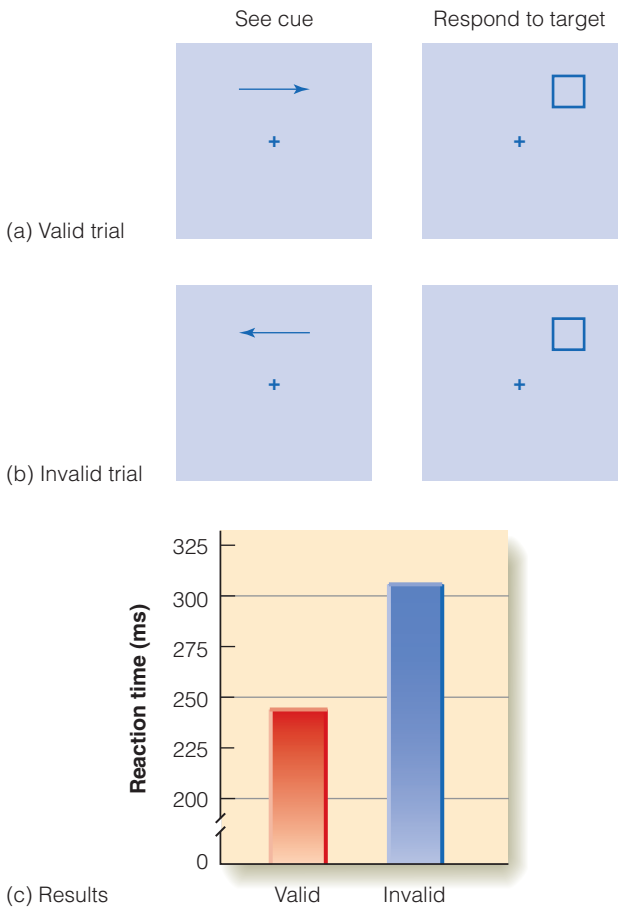

Figure 6.3 Procedure for the (a) valid task and (b) invalid task in Posner and coworkers' (1978) precueing experiment. See text for details. (c) The results of the experiment. The average reaction time was 245 ms for valid trials but 305 ms for invalid trials. (Figures a–b from Posner et al., 1978)

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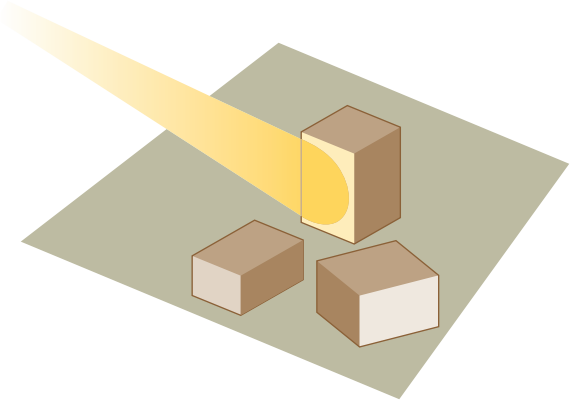

Figure 6.4 Spatial attention can be compared to a spotlight that scans a scene.

at the place where attention is directed. This result and others like it gave rise to the idea that attention operates like a spotlight or zoom lens that improves processing when directed toward a particular location (**Figure 6.4**; Marino & Scholl, 2005).

Attention as a Mechanism for Binding Together an Object's Features: Anne Treisman's Feature Integration Theory

Consider the following stimulus used by Anne Treisman and Hilary Schmidt (1982). A participant briefly saw a display like the one in **Figure 6.5** and was told to report the identity of the black numbers first and then to report what they saw at each of the four locations where the shapes had been. Participants reported the numbers correctly, but on about one-fifth of the trials they reported seeing objects at the other locations that were made up of a combination of features from two different stimuli. For example, after being presented with the display in Figure 6.5, in which the small triangle is red and the small circle is green, they might report seeing a small green triangle. This combination of features is called an **illusory conjunction**.

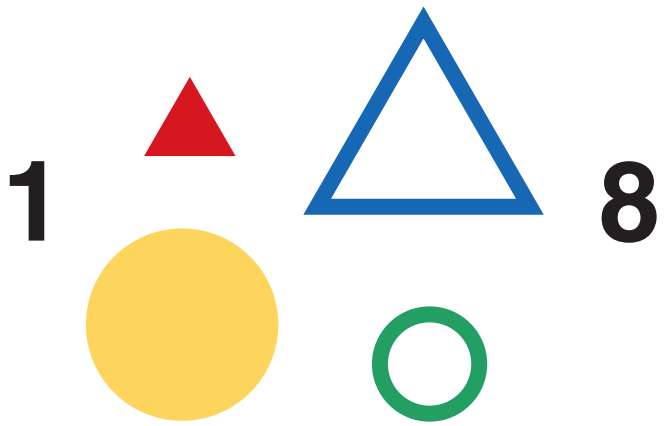

Figure 6.5 Stimuli for Treisman and Schemidt's (1982) experiment. When participants first attended to the black numbers and then to the other objects, some illusory conjunctions, such as "green triangle" occurred.

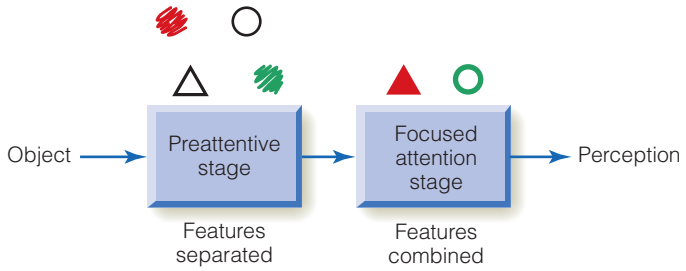

Figure 6.6 Flow diagram of Treisman's (1988) feature integration theory in which features like color and shape exist independently in the preattentive stage and then are combined to create objects in the focused attention stage.

Based on results such as these plus the results of other experiments, Treisman proposed **feature integration theory (FIT)** (Treisman & Gelade, 1980; Treisman, 1985). An early version of the theory, shown in **Figure 6.6**, proposes that the first step in processing an object is the **preattentive stage**. In this stage, features of the object are analyzed rapidly and unconsciously, and at this stage the features exist independently of one another. So the red triangle would be analyzed into independent features "red" and "triangle" and the green circle into "green" and "circular." In the second stage, the **focused attention stage**, attention becomes involved, and conscious perception occurs. Conscious perception involves a process called **binding**, in which individual features are combined, so the viewer sees "red triangle" or "green circle." In other words, during normal viewing, attention combines an object's features so we perceive the object correctly. Illusory conjunctions can occur when attention to the object is distracted, as in the experiment.

Treisman's theory resulted in many experiments supporting the idea of two stages of processing, one unconscious and not involving attention (the preattentive stage) and the other conscious and involving attention (the focused attention stage). One type of experiment used to make this distinction involved a procedure called **visual search**, which is something we do anytime we look for an object among a number of other objects, like trying to find Waldo in a *Where's Waldo?* picture (Handford, 1997).

DEMONSTRATION | Visual Search

In this demonstration, your task is to find a target item that is surrounded by other, distractor, items. First, try finding the horizontal line in **Figure 6.7a**. Then find the horizontal green line in **Figure 6.7b**. The first task is called a feature search, because you could find the target by looking for a single feature, "horizontal." The second task is a conjunction search, because you had to search for a combination (or conjunction) of two or more features, "horizontal" and "green." In this task you couldn't just focus on horizontal, because there were horizontal red bars, and you couldn't just focus on green, because there were vertical green bars. You had to look for the *conjunction* between green and horizontal.

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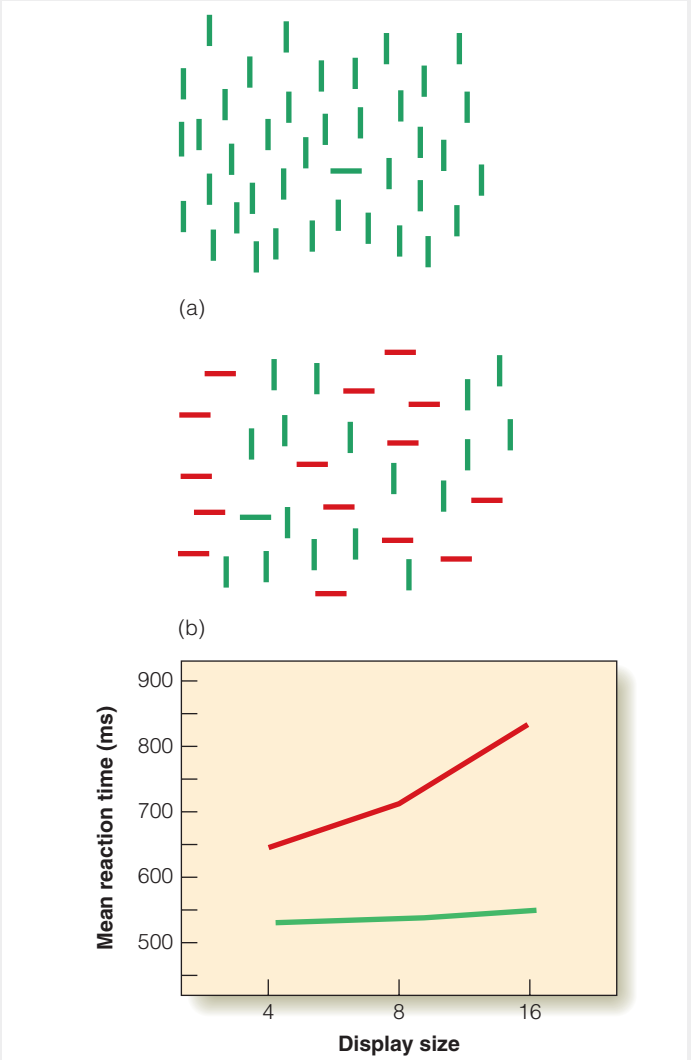

Figure 6.7 Find the horizontal line in (a) and then the green horizontal line in (b). Which task took longer? (c) Typical result of visual search experiments in which the number of distractors is varied for different search tasks. The reaction time for the feature search (green line) is not affected by the number of distractors, but adding distractors increases reaction time for the conjunction search (red line).

This demonstration illustrates the difference between the two stages in Treisman's theory. The feature search was accomplished rapidly and easily because you didn't have to search for the horizontal bar. It just "popped out" of the display. This is an example of automatic processing, which does not require a conscious search. In contrast, the conjunction search did require a conscious search, corresponding to the focused attention stage of FIT, because you had to find the conjunction between two properties.

Treisman demonstrated a difference between the two types of search by having participants find targets, as in the demonstration, and varying the number of distractors. **Figure 6.7c**, which shows the results of a typical experiment of this kind, indicates that the speed of feature search is unaffected by the number of distractors (green line), but the speed of the conjunction search (red line) becomes slower as distractors are added. This difference corresponds to the difference between the rapid preattentive and the slower focused attention stages of FIT.

In a paper commemorating the 40th anniversary of FIT, Arri Kristjansson and Howard Egeth (2019) point out that research during the 40 years since the theory was proposed has not always supported the theory, so that parts of the theory have had to be modified or abandoned. But despite the fact that FIT is now mainly of historical importance, Kristjansson and Egeth point out that FIT was extremely important in early research on attention and that "because of FIT, attention now plays a major role in any account of visual perception."

The work of Cherry, Broadbent, Posner, and Treisman provided evidence that attention is a central process in perception. Broadbent's work was important because it proposed the first flow diagram to explain how attention separates stimuli being attended from stimuli not being attended. Posner's research showed how covert attention can enhance processing of a stimulus. Treisman's research emphasized the role of attention in perceiving coherent objects and also led many other researchers to carry out visual search experiments as a way to study attention.

What all of these early experiments have in common is that they showed, in different ways, how attention can influence perception, and they set the stage for much of the research on attention we will describe in the remainder of this chapter, which focuses on studying (1) the mechanisms that create attention and (2) different ways in which attention influences how we experience our environment. In the next section we will consider an important mechanism that creates attention—the shifting of attention from one place to another by eye movements.

6.3 What Happens When We Scan a Scene by Moving Our Eyes?

Overt attention is attention that occurs when you move your eyes from one place to another. One way to get it touch with the nature of eye movements is to look for things in a scene. Try this by seeing how many birds with white heads you can find in **Figure 6.8**.

Scanning a Scene With Eye Movements

As you looked for the white-headed birds you probably noticed that you had to scan the scene, looking from one place to another. Scanning is necessary because good detail vision occurs only for things which you are looking at directly, as illustrated by the task on page 54, which showed that while looking at the letter on the right, it was difficult to identify the letters to the left.

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Figure 6.8 Count the number of birds that have white heads (no yellow) in this scene.

Bruce Goldstein

This difference occurs because of the way the retina is constructed. Objects you are looking at (central vision) fall on the fovea (see page 41), which has much better detail vision than objects off to the side (peripheral vision), which fall on the peripheral retina. Thus, as you scanned the scene in Figure 6.8, you were aiming your fovea at one object after another. Each time you paused briefly, you were making a **fixation**. When you moved your eye to the next object, you were making a **saccadic eye movement**—a rapid, jerky movement from one fixation to the next.

It isn't surprising that you were moving your eyes from one place to another, because you were trying to find details in the scene. But it may surprise you to know that even when you are freely viewing an object or scene without searching for anything in particular, you move your eyes about three times per second and more than 200,000 times a day. This rapid scanning is shown in **Figure 6.9**, which is a pattern of fixations (yellow dots) separated by saccadic eye movements (lines) that occurred as a participant viewed the picture of the fountain. Note that

Maria Wachala/Getty Images (Scanning measurements by James Brockmole)

Figure 6.9 Scan path of a person freely viewing a picture. Fixations are indicated by the yellow dots and eye movements by the red lines. Notice that this person looked preferentially at some areas of the picture, but is ignoring other areas.

scanning this scene is an example of overt attention, but that covert attention—attending off to the side—is also involved because it helps determine where we are going to look next. Thus, covert attention and overt attention often work together.

How Does the Brain Deal With What Happens When the Eyes Move?

We've seen that eye movements direct our attention to what we want to see. But in the process of shifting the gaze from one place to another, eye movements also do something else: They cause the image on the retina to become smeared. Consider, for example, **Figure 6.10a**, which shows the scan path as a person first fixates on the finger and then moves his eyes to the ear. While this movement of the eyes is shifting overt attention from the finger to the ear, the image of everything located between the finger and ear is sweeping across the retina (**Figure 6.10b**). But we don't see a blurred image. We see a stationary scene. How can that be?

The answer to this question is provided by **corollary discharge theory** (Helmholtz, 1863; Subramanian, et al., 2019; Sun & Goldberg, 2016; von Holst & Mittelstaedt, 1950; Wurtz, 2018). The first step in understanding corollary discharge theory is to consider the following three signals associated with movement of the eyes (**Figure 6.11**).

1. The **motor signal (MS)** occurs when a signal to move the eyes is sent from the brain to the eye muscles.
2. A **corollary discharge signal (CDS)** is a copy of the motor signal, so occurs whenever there is a motor signal.
3. The **image displacement signal (IDS)** occurs when an image moves across the retina, as happens when movement of the eye causes the image of a stationary scene to sweep across the retina (Figure 6.11).

According to corollary discharge theory, the brain contains a structure called the **comparator**. The comparator operates according to the following rule: When only the CDS or the IDS signal reaches it, movement is perceived. But when both signals reach the comparator, no movement is perceived.

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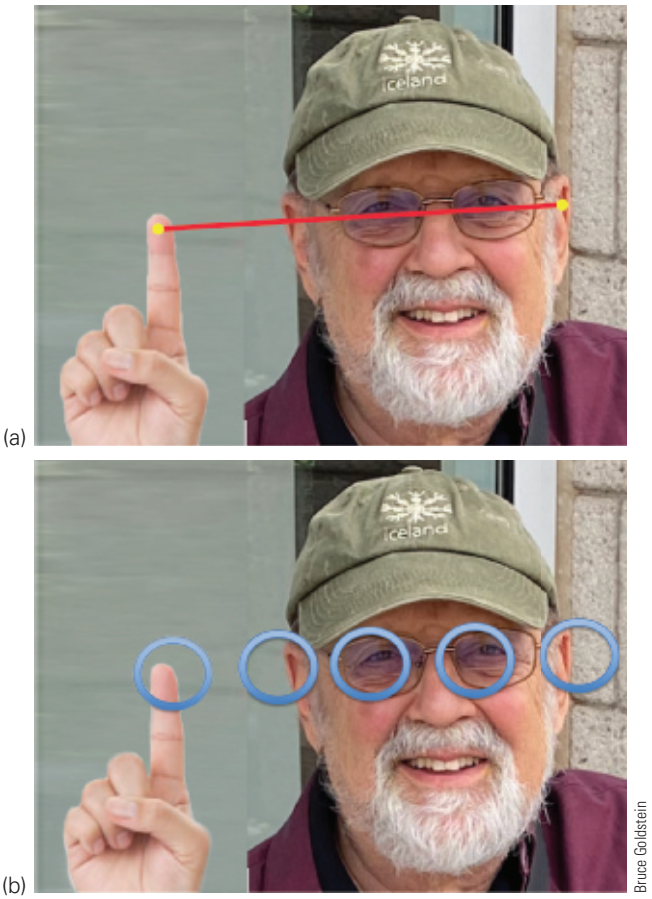

Figure 6.10 (a) Fixation on the person's finger followed by eye movement and then fixation on the person's ear. (b) As the eye moves between the finger and the ear, different images fall on the fovea. Some of these images are indicated by what's inside each circle. Since the eye is moving, these images aren't still images, but smear across the retina as the eye scans from finger to ear.

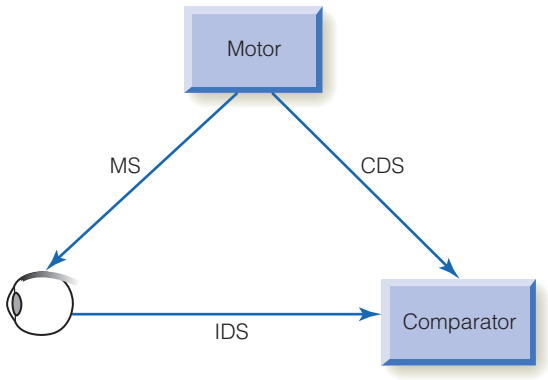

Figure 6.11 Explanation based on corollary discharge theory for why we don't see a smeared image when we move our eyes from one place to another. (1) A motor signal (MS) is sent from the motor area to the eye muscles; (2) the corollary discharge signal (CDS), which is a copy of the motor signal, is sent to the comparator; (3) the eye moves in response to the MS and this movement causes an image to move across the retina, generating an image displacement signal (IDS), which travels out the back of the eye to the comparator, where it meets the CDS. When the IMS meets the CDS, the CDS inhibits perception of the smeared image on the retina caused by movement of the eye.

Because both the CDS and IDS reach the comparator when the eye scans a scene, no movement is perceived, and the scene remains stationary. It should be noted that the comparator is not a single brain area, but involves a number of different structures (Sommer & Wurtz, 2008). The important thing for our purposes is not exactly where the comparator is, but that that there is a mechanism that takes into account both information about stimulation of the receptors and information about movement of the eyes, which determines whether or not movement perception will occur.

According to this mechanism, what should happen if the eyes moved but there was no corollary discharge? In that situation, the comparator receives only one signal—the IDS—so the scene should appear to move. You can create this situation by closing one eye and gently pushing on the eyelid of the other eye, so the eye moves slightly (**Figure 6.12**). When you do this, there is an IDS, because the eye is moving, but there is no CDS, because no signal is being sent to the eye muscles. Because the comparator receives just one signal, the scene appears to move. Imagine how disturbing it would be if this kind of movement occurred each time your eyes moved while scanning a scene. Luckily, information provided by the CD helps keep our world stationary as our eyes move throughout a scene (Wurtz, 2013).

Although the CD solves the problem of the smeared retinal image by alerting the brain that the eye is moving, movement of the eyes also causes another problem: Each eye movement causes the scene to change. First there's a finger in the center of a scene, then moments later an ear appears, and a moment after that, something else takes center stage. Thus, what happens on the retina is like a series of snapshots that are somehow processed so we see not "snapshots" but a stationary scene.

Luckily, the corollary discharge not only keeps our world stationary as our eyes move, but it also deals with the snapshot problem by helping the brain prepare for what is coming next. Martin Rolfs and coworkers (2011) determined this

Figure 6.12 Why is this woman smiling? Because when she pushes on her eyelid, so her eye moves, she sees the world jiggle.

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by measuring participants' ability to judge the slant of a line flashed near a target where they were going to move their eyes. They found that the participants' performance on the slant task began to increase *before* the eye began moving toward the target. This result, combined with the results of many physiological experiments, shows that attention begins shifting toward the target just before the eye begins moving toward it, a phenomenon called the **predictive remapping of attention** (Melcher, 2007; Rao et al., 2016). Although the details of this process remain to be worked out, this remapping appears to be one of the reasons that we see a stable, coherent scene, even though it is based on a series of "snapshots" on the retina.

6.4 Things That Influence Visual Scanning

William James's statement, "Attention involves withdrawing from some things in order to effectively deal with others" leads to the question, "what causes us to direct our attention toward things we want to deal with and away from things we want to withdraw from?" We will answer this question by describing a number of things that influence where people shift their attention by moving their eyes.

Visual Salience

Some things in the world draw our attention because they stand out against their backgrounds. For example, the man in the red shirt in **Figure 6.13** is conspicuous because his shirt's color starkly contrasts with the whites and pale blues worn by everyone else in the scene. Scene regions that are markedly different from their surroundings, whether in color, contrast, movement, or orientation, are said to have **visual salience**. Visually salient objects can attract attention, as you will see in the following demonstration.

Ales Fevzer/CORBIS

Figure 6.13 The red shirt is highly salient because it is bright and contrasts with its surroundings.

DEMONSTRATION | Attentional Capture

Each shape in **Figure 6.14** contains a vertical or horizontal line. What is the orientation of the line inside the green circle? Answer this question before reading further.

Figure 6.14. An example of attention capture: When participants are instructed to find the green circle, they often look at the red diamond first. (Theeuwes, 1992)

It probably wasn't too difficult to find the green circle and to determine that it contains a horizontal line. But did you look at the red diamond first? Most people do. The question is, why would they do so? You were asked to find a green circle, and the red diamond is neither green nor a circle. Regardless, people attend to the red diamond because it is highly salient, and salient items attract people's attention (Theeuwes, 1992). Researchers use the term **attentional capture** to describe situations like this, in which properties of a stimulus grab attention, seemingly against a person's will. Even though attentional capture can distract us from what we want to be doing, capture is an important means of directing attention because conspicuous stimuli like rapid movement or loud sounds can capture our attention to warn us of something dangerous like an animal or object moving rapidly toward us.

To investigate how visual salience influences attention in scenes that do not contain a single salient object, researchers have developed an approach in which they analyze characteristics such as color, orientation, and intensity at each location in a scene and combine these values to create a **saliency map** of the scene. A saliency map reveals which regions are visually different from the rest of the scene (Itti & Koch, 2000; Parkhurst et al., 2002; Torralba et al., 2006). **Figure 6.15** shows a scene (a) and its saliency map (b) as determined by Derrick Parkhurst and coworkers (2002). Regions of greater visual salience are

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denoted by brighter regions in the saliency map. Notice how the surf in **Figure 6.15a** is indicated as particularly salient in **Figure 6.15b**. This is because the surf constitutes an abrupt change in color, brightness, and texture relative to the sky, beach, and ocean. The clouds in the sky and the island on the horizon are also salient for similar reasons. When Parkhurst and coworkers calculated saliency maps for a number of pictures and then measured observers' fixations as they observed the pictures, they found that the first few fixations were more likely to occur on high-saliency areas. After the first few fixations, however, scanning begins to be influenced by cognitive processes that depend on things such as an observer's interests and goals. As we will see in the next section, interests and goals are influenced by the observer's past experiences in observing the environment.

The Observer's Interests and Goals

One way to show that where we look isn't determined only by saliency is by checking the eye movements of the participant looking at the fountain in Figure 6.9. Notice that this person never looked at the bright blue water, even though it is very salient due to its brightness, color, and position near the front of the scene. This person also ignored the rocks, columns, windows, and several other prominent architectural features. Instead, this person focused on aspects of the fountain that he or she found more interesting, such as the statues. It is likely that the *meaning* of the statues has attracted this particular person's attention. It is important to note, however, that just because this person spent most of his or her time looking at the statues doesn't mean everyone would. Just as there are large variations between people, there are variations in how people scan scenes (Castelhano & Henderson, 2008; Noton & Stark, 1971). Thus, another person, who might be interested in the architecture of the buildings, might look less at the statues and more at the building's windows and columns.

(a) Visual scene

(b) Saliency map

Vision Research/Elsevier

Figure 6.15 (a) A visual scene. (b) Saliency map of the scene determined by analyzing the color, contrast, and orientations in the scene. Lighter areas indicate greater salience. (Adapted from Parkhurst et al., 2002)

Attention can also be influenced by a person's goals. In a classic demonstration, Alfred Yarbus (1967) recorded participants' eye movements while they were told to just look at Repin's painting *An Unexpected Visitor* (**Figure 6.16a**), or to determine the ages of the people (**Figure 6.16b**), to remember the people's clothing (**Figure 6.16c**), or to remember the position of the people and objects (**Figure 6.16d**). It is clear from the eye movement records that the patterns of eye movements depended on the information participants were told to remember.

More recent work has shown that people's interests and goals can actually be decoded from their eye movements (Borji & Itti, 2014). For example, John Henderson and coworkers (2013) recorded the eye movements of participants who either searched for a specific object in a scene or who tried to memorize the entire scene for a later test. After the experiment, the researchers were able to correctly guess the participants' task on each trial simply by examining their eye movements. Clearly, as people's intentions and tasks change, they will change how they focus their attention on a scene.

Scene Schemas

Attention is also influenced by **scene schemas**—an observer's knowledge about what is contained in typical scenes (remember our discussion of regularities of the environment in Chapter 5, page 105). Thus, when Melissa Võ and John Henderson (2009) showed pictures like the ones in **Figure 6.17**, observers looked longer at the printer in **Figure 6.17a** than the pot in **Figure 6.17b** because a printer is less likely to be found in a kitchen. The fact that people look longer at things that seem out of place in a scene means that attention is being affected by their knowledge of what is usually found in the scene.

Another example of how cognitive factors based on knowledge of the environment influences scanning is an experiment by Hiroyuki Shinoda and coworkers (2001) in which they measured observers' fixations and tested their ability to detect traffic signs as they drove through a computer-generated environment in a driving simulator. They found that the observers were more likely to detect stop signs positioned at intersections than those positioned in the middle of a block, and

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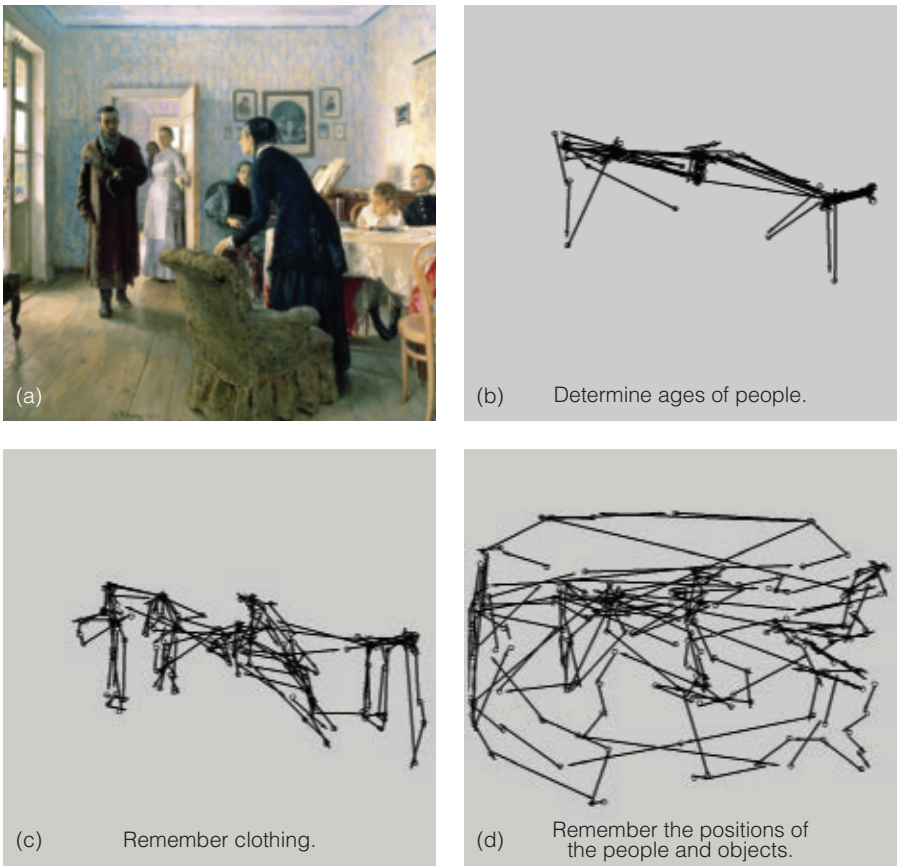

Unexpected, 1884–88 (oil on canvas), Repin, Ilya Efimovich (1844-1930)/Tretyakov Gallery, Moscow, Russia/Bridgeman Images; Lucs-kho

Figure 6.16 Yarbus (1967) asked participants to view the painting in (a) and recorded their eye movements while they either (b) determined the ages of the people, (c) had to remember the clothes worn by the people, or (d) had to remember the positions of the people and objects in the room. The scan paths show that subjects' eye movements are strongly influenced by the task.

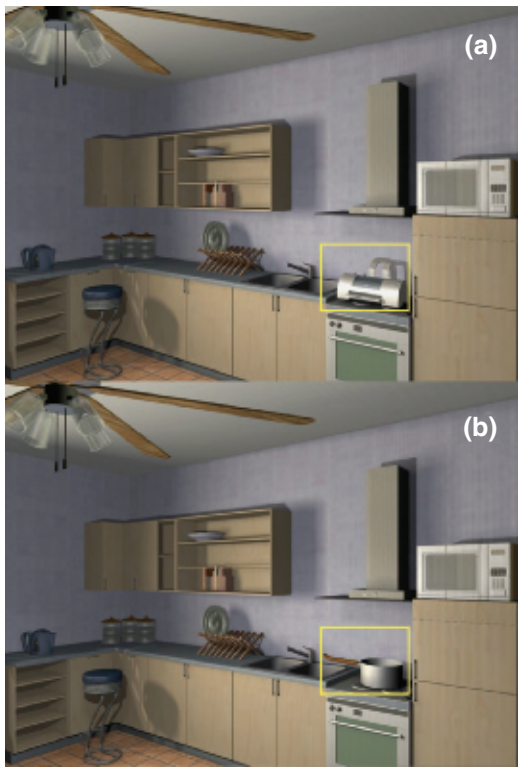

Figure 6.17 Stimuli used by Vo and Henderson (2009). Observers spent more time looking at the printer in (a) than at the pot in (b), shown inside the yellow rectangles (which were not visible to the observers).

that 45 percent of the observers' fixations occurred close to intersections. In this example, the observers are using learning about regularities in the environment (stop signs are usually at corners) to determine when and where to look for stop signs.

Task Demands

The examples in the last section demonstrate that knowledge of various characteristics of the environment can influence how people direct their attention. However, the last example, in which participants drove through a computer-generated environment, was different from the rest. The difference is that instead of looking at pictures of stationary scenes, participants were interacting with the environment. This kind of situation, in which people are shifting their attention from one place to another as they are doing things, occurs when people are moving through the environment, as in the driving example, and when people are carrying out specific tasks.

Because many tasks require shifting attention to different places as the task unfolds, it isn't surprising that the timing of when people look at specific places is determined by the sequence of actions involved in the task. Consider, for example, the pattern of eye movements in **Figure 6.18**, which were measured as a person was making a peanut butter sandwich. The process of making the sandwich begins by removing a slice of bread from the bag and putting it on the plate. This operation is accompanied by an eye movement from the bag to the plate.

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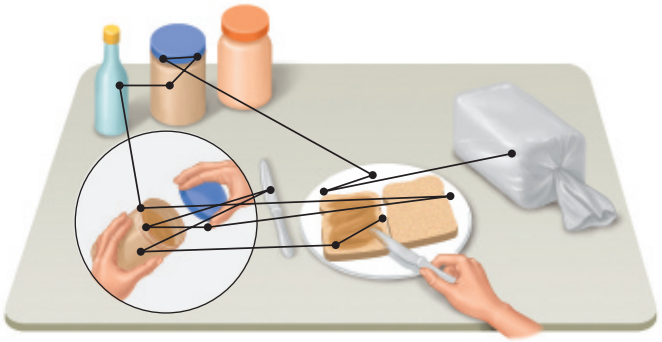

Figure 6.18 Sequence of fixations of a person making a peanut butter sandwich. The first fixation is on the loaf of bread. (From Land & Hayhoe, 2001)

The observer then looks at the peanut butter jar just before it is lifted and looks at the top just before it is removed. Attention then shifts to the knife, which is picked up and used to scoop the peanut butter and spread it on the bread (Land & Hayhoe, 2001).

The key finding of these measurements, and also of another experiment in which eye movements were measured as a person prepared tea (Land et al., 1999), is that the person's eye movements were determined primarily by the task. The person fixated on few objects or areas that were irrelevant to the task, and eye movements and fixations were closely linked to the action the person was about to take. Furthermore, the eye movement usually preceded a motor action by a fraction of a second, as when the person first fixated on the peanut butter jar and then reached over to pick it up. This is an example of the "just in time" strategy—eye movements occur just before we need the information they will provide (Hayhoe & Ballard, 2005; Tatler et al., 2011).

The examples we have described in connection with scanning based on cognitive factors and task demands have something in common: They all provide evidence that scanning is influenced by people's *predictions* about what is likely to happen (Henderson, 2017). Scanning anticipates what a person is going to do next as they make a peanut butter and jelly sandwich; scanning anticipates that stop signs are most likely to be located at intersections; and pausing scanning to look longer at an object occurs when a person's expectations are violated, as when a printer unexpectedly appears in a kitchen.

TEST YOURSELF 6.1

1. What are the two main points that William James makes about attention? (Hint: what it is and what it does.) What are two reasons for paying attention to some things and ignoring others?
2. Define attention, overt attention, and covert attention.
3. Describe Cherry's dichotic listening experiment. What did it demonstrate?
4. What is the central feature of Broadbent's model of attention?
5. What is spatial attention? Describe Posner's experiment on speeding response to locations. Be sure you understand the precueing procedure, covert attention, and what Posner's results demonstrated.
6. What does feature integration theory propose?
7. Describe two types of visual search: feature search and conjunction search. How are these two types of searches affected by the number of distractors in a display?
8. How do these two types of searches relate to the two stages of Treisman's feature integration theory?
9. What is the difference between central vision and peripheral vision and how is this relevant to eye movements?
10. What are fixations? Saccadic eye movements?
11. Describe how the corollary discharge theory explains why we don't see a scene as smeared when we move our eyes.
12. Why does the scene appear to move when we push on our eyelid?
13. Describe predictive remapping of attention. Why is it necessary?
14. Describe the following factors that determine where we look: visual salience, observer goals, scene schemas, and scanning based on task demands. Describe the examples or experiments that illustrate each factor.

6.5 The Benefits of Attention

What do we gain by attending? Based on our description of overt attention that is associated with eye movements, we might answer that question by stating that shifting attention by moving our eyes enables us to see places of interest more clearly. This is extremely important, because it places the things we're interested in front-and-center where they are easy to see.

But some researchers have approached attention not by measuring factors that influence eye movements, but by considering what happens during covert attention, when attention is shifted without making eye movements, as occurred in Posner's precueing experiments that we described at the beginning of the chapter (p. 125).

One reason Posner studied covert attention is that it is a way of studying what is happening in the mind without the interference of eye movements. We will now consider more recent research on covert attention, which shows how shifting attention "in the mind" can affect how quickly we can respond to locations and to objects, and how we perceive objects.

Attention Speeds Responding

Posner's precueing study showed how covert attention resulted in faster responding to the cued locations. We will now

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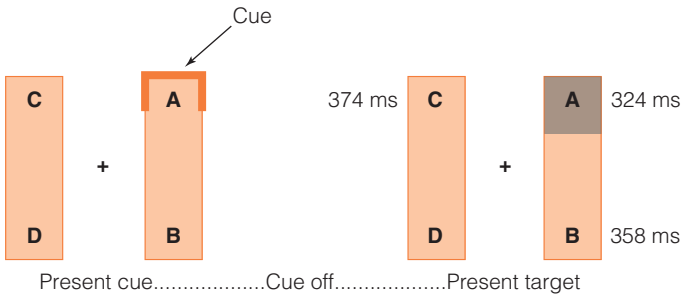


Figure 6.19 In Egley and coworkers' (1994) experiment, (a) a cue signal appears at one place on the display, then the cue is turned off and (b) a target is flashed at one of four possible locations, A, B, C, or D. Numbers are reaction times in ms for positions A, B, and C, when the cue appeared at position A. (From Egly et al., 1994)

consider some experiments that show (1) that when attention is directed to one part of an object, the enhancing effect of that attention spreads to other parts of the object, and (2) that attention can influence appearance. Consider, for example, the experiment diagrammed in **Figure 6.19** (Egly et al., 1994). As participants kept their eyes on the +, one end of the rectangle was briefly highlighted (**Figure 6.19a**). This was the cue signal that indicated where a target, a dark square (**Figure 6.19b**), would probably appear. In this example, the cue indicates that the target is likely to appear in position A, at the upper part of the right rectangle. (The letters used to illustrate positions in our description did not appear in the actual experiment.)

The participants' task was to press a button when the target was presented anywhere on the display. The numbers indicate their average reaction times, in milliseconds, for three target locations when the cue signal had been presented at A. Not surprisingly, participants responded most rapidly when the target was presented at A, where the cue had been presented. However, the most interesting result is that participants responded more rapidly when the target was presented at B (reaction time = 358 ms) than when the target was presented at C (reaction time = 374 ms). Why does this occur? It can't be because B is closer to A than C, because B and C are exactly the same distance from A. Rather, B's advantage occurs because it is located *within the object* that was receiving the participant's attention. Attending at A, where the cue was presented, causes the maximum effect at A, but the effect of this attention spread throughout the object so some enhancement occurred at B as well. The faster responding that occurs when enhancement spreads within an object is called the **same-object advantage** (Marino & Scholl, 2005).

Attention Influences Appearance

Does the fact that attention can result in faster reaction times show that attention can change the *appearance* of an object? Not necessarily. It is possible that the target stimulus always looks the same, but attention enhances the observer's ability to press the button quickly. To answer the question of whether attention affects an object's appearance, we need to do an experiment that measures the *perceptual response* to a stimulus rather than the *speed of responding* to the stimulus.

In a paper titled "Attention Alters Appearance," Marisa Carrasco and coworkers (2004) showed that attention affected the perceived contrast between the alternating light and dark bars like the ones in **Figure 6.20c**, where **perceived contrast** refers to how different the light and dark bars appear.

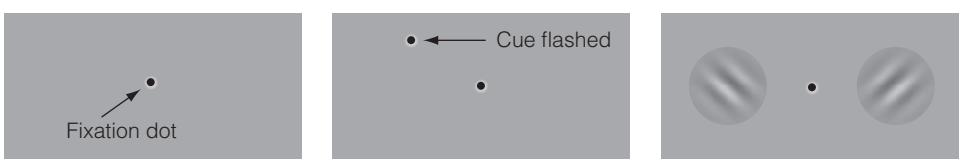
The procedure for Carrasco's experiment, shown in **Figure 6.20**, was as follows:

(a) Participants were instructed to keep their eyes fixed on the small fixation dot at all times.
(b) A cue dot was flashed for 67 ms either on the left or on the right. Even though participants were told that this dot wasn't related to what happened next, it functioned to shift their covert attention to the left or to the right.
(c) A pair of gratings, one tilted to the left and the other tilted to the right, was flashed for 40 ms. The contrast between the bars of the gratings was randomly varied from trial to trial, so sometimes the contrast of the right grating was higher, sometimes the contrast of the left grating was higher, and sometimes the two gratings were identical. The participants indicated, by pressing a key, whether the grating stimulus with the highest contrast was tilted to the left or to the right.

Carrasco found that when two gratings were physically identical, participants were more likely to report the orientation of the one that was on the same side as the flashed cue dot. Thus, even though the two gratings were the same, the one that received attention appeared to have more contrast (see also Liu et al., 2009).

In addition to perceived contrast, a variety of other perceptual characteristics are affected by attention. For example, attended objects are perceived to be bigger, faster, and more richly colored (Anton-Erxleben et al., 2007; Fuller & Carrasco, 2006; Turatto et al., 2007), and attention increases visual acuity—the sharpness of vision (Montagua et al., 2009). Thus, more than 100 years after William James suggested that attention makes an object "clear and vivid," researchers have provided experimental evidence that attention does, in fact, enhance the appearance of an object. (See Carrasco & Barbot, 2019.)

Figure 6.20 Procedure for Carrasco and coworkers' (2004) experiment. See text for explanation.



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From the experiments we have described, it is clear that attention can affect both how a person *responds* to a stimulus and how a person *perceives* a stimulus. It should be no surprise that these effects of attention are accompanied by changes in physiological responding.

6.6 The Physiology of Attention

A large number of experiments have shown that attention affects physiological responding in a variety of ways. We begin by considering evidence that attention increases the neural response to an attended item.

Attention to Objects Increases Activity in Specific Areas of the Brain

In an experiment by Kathleen O'Craven and coworkers (1999), participants saw a face and a house superimposed (**Figure 6.21a**). You may remember the experiment from Chapter 5 in which a picture of a house was presented to one eye and a picture of a face was presented to the other eye (see Figure 5.47, page 114). In that experiment, presenting different images to each eye created binocular rivalry, so perception alternated between the two images. When the face was perceived, activation increased in the fusiform face area (FFA). When the house was perceived, activation increased in the parahippocampal place area (PPA).

In O'Craven's experiment, the superimposed face and house stimuli were presented to both eyes, so there was no binocular rivalry. Instead of letting rivalry select the image that is visible, O'Craven told participants to direct their attention to one stimulus or the other. For each pair, one of the stimuli was stationary and the other was moving slightly back and forth. When looking at a pair, participants were told to attend to either the moving or stationary house, the moving or stationary face, or to the direction of movement. As they were doing this, activity in their FFA, PPA, and MT/MST (an area specialized for movement that we will discuss in Chapter 8) was measured.

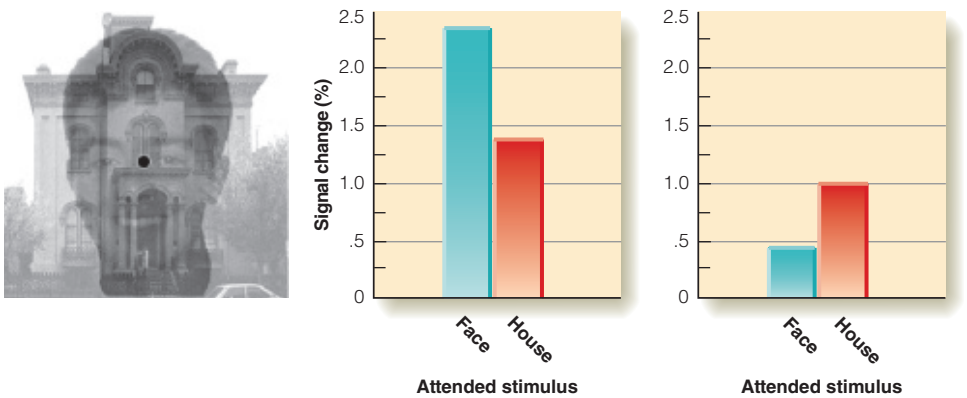
The results for when participants attended to the house or the face show that attending to the moving or stationary *face* caused enhanced activity in the FFA (**Figure 6.21b**) and attending to the moving or stationary *house* caused enhanced activity in the PPA (**Figure 6.21c**). In addition, attending to the movement caused activity in the movement areas, MT/MST, for both moving face and moving house stimuli. Thus, attention to different types of objects influences the activity in areas of the brain that process information about that type of object (see also Çukur et al., 2013).

Attention to Locations Increases Activity in Specific Areas of the Brain

What happens in the brain when people shift their attention covertly to different locations while keeping their eyes stationary? Ritobrato Datta and Edgar DeYoe (2009; see also Chiu & Yantis, 2009) answered this question by measuring how brain activity changed when covert attention was focused on different locations. They measured brain activity using fMRI as participants kept their eyes fixed on the center of the stimulus shown in **Figure 6.22a** and shifted their attention to different locations within the display. Because the eyes did not move, the visual image on the retina did not change. Nevertheless, they found that patterns of activity within the visual cortex changed depending on where a participant was directing his or her attention.

The colors in the circles in **Figure 6.22b** indicate the area of brain that was activated when a participant directed his attention to the locations indicated by the letters on the stimulus in Figure 6.19a. Notice that the yellow "hot spot," which is the place of greatest activation, is near the center when the participant is paying attention to area A, near where he is looking. But shifting his attention to areas B and C, while keeping the eyes stationary, causes the increase in brain activity to move out from the center.

By collecting brain activation data for all of the locations on the stimulus, Datta and DeYoe created "attention maps" that show how directing attention to a specific area of space activates a specific area of the brain. These attention maps are like the retinotopic map we described in Chapter 4



(a) Stimulus (b) FFA Activity (c) PPA Activity

Figure 6.21 (a) Superimposed face and house stimulus used in O'Craven and coworkers' (1999) experiment. (b) FFA activation when the subject attended to the face or the house. (c) PPA activation for attention to the face or the house. (Based on data from O'Craven et al., 1999)

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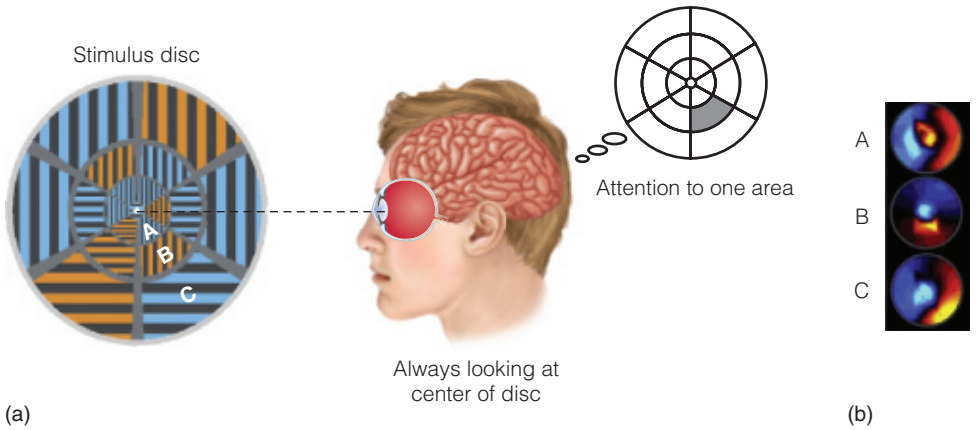

Figure 6.22 (a) Participants in Datta and DeYoe's (2009) experiment directed their attention to different areas of this circular display while keeping their eyes fixed on the center of the display. (b) Activation of the brain that occurred when the participants attended to the areas indicated by the letters on the stimulus disc. The center of each circle is the place on the brain that corresponds to the center of the stimulus. The yellow "hot spot" is the area of the brain that is maximally activated by attention. (Datta & DeYoe, 2009)

(see Figure 4.12, page 75), in which presenting objects at different locations on the retina activates different locations on the brain. However, in Datta and DeYoe's experiment, brain activation is changing not because images are appearing at different places on the retina, but because the participant is directing his or her mind to different places in the visual field.

What makes this experiment even more interesting is that after attention maps were determined for a particular participant, that participant was told to direct his or her attention to a "secret" place, unknown to the experimenters. Based on the location of the resulting yellow "hot spot," the experimenters were able to predict, with 100 percent accuracy, the "secret" place where the participant was attending. This is similar to the "mind reading" experiment we described in Chapter 5, in which brain activity caused by an oriented line was analyzed to determine what orientation the person was seeing (see Figure 5.48, page 115). In the attention experiments, brain activity caused by *where the person was attending* was analyzed to determine where the person was directing his or her mind!

Attention Shifts Receptive Fields

In Chapter 4 we showed how presenting vertical bars outside a neuron's receptive field can increase the *rate of firing* to a vertical bar located inside the receptive field (see Figure 4.33, page 86). We now describe a situation in which attention can shift the *location* of a neuron's receptive field. Theo Womelsdorf and coworkers (2006) demonstrated this by recording from neurons in a monkey's temporal lobe. **Figure 6.23a** shows the location of a neuron's receptive field when the monkey was keeping its eyes fixed on the white dot, but was paying attention to the diamond location indicated by the arrow. **Figure 6.23b** shows how the location of the receptive field shifted when the monkey's attention shifted to the circle location indicated by the arrow. In both of these examples, yellow indicates the area of the retina that, when stimulated, causes the greatest response.

This shifting of the receptive field, depending on where the monkey is attending, is an amazing result because it means that attention is changing the organization of part of the visual system. Receptive fields, it turns out, aren't fixed in place but can change in response to where the monkey is paying

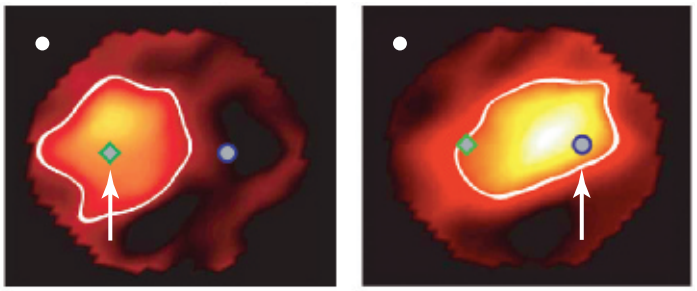

Figure 6.23 Receptive field maps on the retina determined when a monkey was looking at the fixation spot (white) but paying attention to locations indicated by the arrows: (a) the diamond or (b) the circle. The arrows were not included in the display seen by the monkey. The yellow areas are areas of the receptive field that generate the largest response. Notice that the receptive field map shifts to the right when the monkey shifts its attention from the diamond to the circle. (From Womelsdorf et al., 2006)

attention. This concentrates neural processing power at the place that is important to the monkey at that moment. As we continue exploring how the nervous system creates our perceptions, we will encounter other examples of how the flexibility of our nervous system helps us function within our ever-changing environment.

6.7 What Happens When We Don't Attend?

We have seen that paying attention affects both responding to stimuli and perceiving them. But what happens when we don't pay attention? One idea is that you don't perceive things you aren't attending to. After all, if you're looking at something over to the left, you're not going to see something else that is far to the right. But research has shown not only that we miss things that are out of our field of view, but that not attending can cause us to miss things even if we are looking directly at them. One example of this is a phenomenon called **inattentional blindness**.

In 1998, Arien Mack and Irvin Rock published a book titled *Inattentional Blindness*, in which they described experiments

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that showed that participants can be unaware of clearly visible stimuli if they aren't directing their attention to them. In an experiment based on one of Mack and Rock's experiments, Ula Cartwright-Finch and Nilli Lavie (2007) presented the cross stimulus shown in **Figure 6.24**. The cross was presented for five trials, and the participants' task was to indicate which arm of the briefly flashed cross was longer, the horizontal or the vertical. This was a difficult task because the cross was flashed rapidly, the arms were just slightly different in length, and the arm that was longer changed from trial to trial. On the sixth trial, a small outline of a square was added to the display (**Figure 6.24b**). Immediately after the sixth trial, participants were asked whether they noticed if anything had appeared on the screen that they had not seen before. Out of 20 participants, only 2 reported that they had seen the square. In other words, most of the participants were "blind" to the small square, even though it was located right next to the cross.

This demonstration of inattentional blindness used a rapidly flashed geometric test stimulus. But similar effects occur for more naturalistic stimuli that are visible for longer periods of time. For example, imagine looking at a display in a department store window. When you focus your attention on the display, you probably fail to notice the reflections on the surface of the window. Shift your attention to the reflections, and you become less aware of the display inside the window.

The idea that attention can affect perception of overlapping scenes was tested in an experiment by Daniel Simons and Christopher Chabris (1999), who created a 75-second film that showed two "teams" of three players each. One team, dressed in white, was passing a basketball around, and the other was "guarding" that team by following them around and putting their arms up as in a basketball game (**Figure 6.25**). Participants were told to count the number of passes, a task that focused their attention on the team wearing white. After about 45 seconds, one of two events occurred. Either a woman carrying an umbrella or a person in a gorilla suit walked through the "game," an event that took 5 seconds.

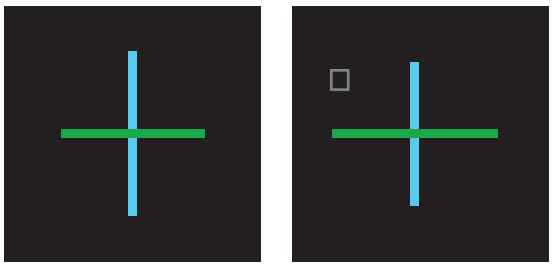

Figure 6.24 Inattentional blindness experiment. (a) The cross display is presented for five trials. One arm of the cross is slightly longer on each trial. The participant's task is to indicate which arm (horizontal or vertical) is longer. (b) On the sixth trial, the participants carry out the same task, but a small square is included in the display. After the sixth trial, participants are asked if they saw anything different than before. (From Cartwright-Finch & Lavie, 2007; Lavie, 2010)

Bruce Goldstein

Figure 6.25 Frame from Simons and Chabris's (1999) experiment.

After seeing the video, participants were asked whether they saw anything unusual happen or whether they saw anything other than the six players. Nearly half of the observers failed to report that they saw the woman or the gorilla. This experiment demonstrated that when people are attending to one sequence of events, they can fail to notice another event, even when it is right in front of them (also see Goldstein & Fink, 1981; Neisser & Becklen, 1975).

Following in the footsteps of inattentional blindness experiments, researchers developed another way to demonstrate how a lack of attention can affect perception. Instead of presenting several stimuli at the same time, they first presented one picture, then another slightly different picture. To appreciate how this works, try the following demonstration.

DEMONSTRATION | Change Detection

When you are finished reading these instructions, look at the picture in **Figure 6.26** for just a moment, and then turn the page and see whether you can determine what is different in **Figure 6.27**. Do this now.

Bruce Goldstein

Figure 6.26 Stimulus for change-blindness demonstration. See text.

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Figure 6.27 Stimulus for change-blindness demonstration. See text.

Were you able to see what was different in the second picture? People often have trouble detecting the change even though it is obvious when you know where to look. (See the bottom of page 146 for a hint and then try again.) Ronald Rensink and coworkers (1997) did a similar experiment in which they presented one picture, followed by a blank field, followed by the same picture but with an item missing, followed by a blank field, followed by the original picture, and so on. The pictures were alternated in this way until observers were able to determine what was different about them. Rensink found that the pictures had to be alternated back and forth a number of times before the difference was detected. This difficulty in detecting changes in scenes is called **change blindness** (Rensink, 2002).

Change blindness occurs regularly in popular films, in which some aspect of the scene, which should remain the same, changes from one shot to the next. In the *Wizard of Oz* (1939), Dorothy's (Judy Garland's) hair changes length many times from short to long and back again. In *Pretty Woman* (1990) Vivian (Julia Roberts) began to reach for a croissant for breakfast that suddenly turned into a pancake. And magically, in *Harry Potter and the Sorcerer's Stone* (2001) Harry (Daniel Radcliffe) suddenly changed where he was sitting from one shot to the next during a conversation in the Great Hall. These changes in films, called **continuity errors**, have been well documented on the Internet (search for "continuity errors in movies").

The message of the change blindness and inattentional blindness experiments is that when we are paying attention to one thing, we miss other things. Although change blindness and inattentional blindness were determined in laboratory experiments, there are many examples in real life of things that distract us by grabbing our attention. A major perpetrator of this distraction is the smartphone, which has been accused of being "the prime culprit in hijacking attention" (Budd, 2017).

6.8 Distraction by Smartphones

Perhaps the most studied effect of smartphone distractions involves the effect on driving. We consider this first, and then will describe how smartphone distraction affects other activities.

Smartphone Distractions While Driving

Driving presents a paradox: in many cases, we are so good at it that we can operate on "auto-pilot," as when we are driving down a straight highway in light traffic. However, in other cases, driving can become very demanding, as when traffic increases or hazards suddenly present themselves. In this latter case, distractions that result in a decrease in attention to driving are particularly dangerous.

The seriousness of driver inattention was verified by a research project called the 100-Car Naturalistic Driving Study (Dingus et al., 2006). In this study, video recorders in 100 vehicles created records of both what the drivers were doing and the view out the front and rear windows. These recordings documented 82 crashes and 771 near crashes in more than 2 million miles of driving. In 80 percent of the crashes and 67 percent of the near crashes, the driver was inattentive in some way 3 seconds beforehand. One man kept glancing down and to the right, apparently sorting through papers in a stop-and-go driving situation, until he slammed into an SUV. A woman eating a hamburger dropped her head below the dashboard just before she hit the car in front of her. One of the most distracting activities was pushing buttons on a smartphone or similar device. More than 22 percent of near crashes involved that kind of distraction, and it is likely that this number may be higher now because of increases in smartphone use since that study.

In a laboratory experiment on the effects of smartphones, David Strayer and William Johnston (2001) gave participants a simulated driving task that required them to apply the brakes as quickly as possible in response to a red light. Doing this task while talking on a phone caused participants to miss twice as many of the red lights as when they weren't talking on the phone (**Figure 6.28a**) and also increased the time it took them to apply the brakes (**Figure 6.28b**). Perhaps the most important finding of this experiment is that the same decrease in performance occurred regardless of whether participants used a hands-free or a handheld device.

Taking into account results such as these, plus many other experiments on the effects of phones on driving, Strayer and coworkers (2013) concluded that talking on the phone uses mental resources that would otherwise be used for driving the car (also see Haigney & Westerman, 2001; Lamble et al., 1999; Spence & Read, 2003; Violanti, 1998). This conclusion that the problem posed by phone use during driving is related to the use of mental resources is an important one. The problem isn't driving with one hand. It is driving with fewer mental resources available to focus on driving.

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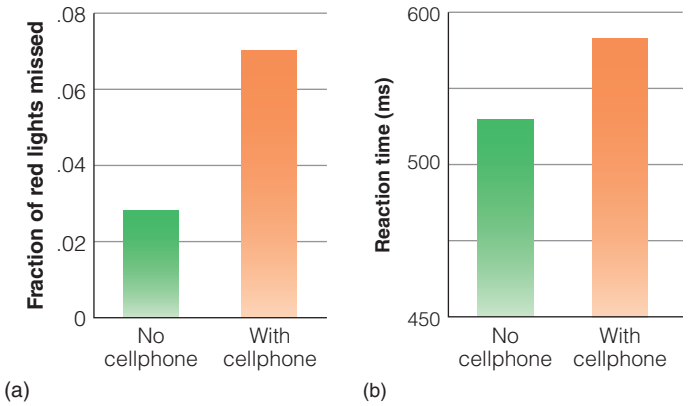

Figure 6.28 Results of Strayer and Johnston's (2001) cellphone experiment. When participants were talking on a cellphone, they (a) missed more red lights and (b) took longer to apply the brakes. (From Strayer & Johnston, 2001)

But even though research clearly shows that driving while talking on a phone is dangerous, many people believe it doesn't apply to them. For example, in response to a class assignment, one of my students wrote, "I do not believe my driving is affected by talking on the phone ... My generation learned to drive when cell phones were already out. I had one before driving, so while learning to drive, I also simultaneously learned to talk on the phone and drive." Thinking such as this may be why 27 percent of adults report that they sometimes text while driving, even in the face of overwhelming evidence that it is dangerous (Seiler, 2015; Wiederhold, 2016). For example, a study by the Virginia Tech Transportation Institute found that truck drivers who send text messages while driving were 23 times more likely to cause a crash or near crash than truckers who were not texting (Olson et al., 2009). Because of results such as these, which indicate that texting is even more dangerous than talking on a phone, most states now have laws against text-messaging while driving.

The main message here is that anything that distracts attention can degrade driving performance. And phones aren't the only attention-grabbing device found in cars. Most cars now feature screens that can display the same apps that are on your phone. Some voice-activated apps enable drivers to make movie or dinner reservations, send and receive texts or emails, and create posts on Facebook. An early system in Ford vehicles was called an "infotainment system." But a study from the AAA Foundation for Traffic Safety, *Measuring Cognitive Distraction in the Automobile*, indicates that perhaps too much information and entertainment while driving isn't a good thing. The study found that voice-activated activities were more distracting, and therefore potentially more dangerous, than either hands-on or hands-free phones. The study concludes that "just because a new technology does not take the eyes off the road does not make it safe to be used while the vehicle is in motion" (Strayer et al., 2013).

Research such as this shows that attention affects not only where we are looking as we are driving, but also how we are thinking. But media's effect on attention has extended far beyond driving, as indicated by scenes like the one in **Figure 6.29**, which shows that you don't have to be in a car to have your attention captured by your phone! We now consider research which shows that phones, and the Internet in general, can have negative effects on many aspects of our behavior.

Distractions Beyond Driving

> The proliferation of smartphones has ushered in an era of unprecedented connectivity. Consumers around the globe are now constantly connected to faraway friends, endless entertainment, and virtually unlimited information ... Just a decade ago, this state of constant connection would have been inconceivable; today, it is seemingly indispensable. (Ward et al., 2017)

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Figure 6.29 City scene showing people walking and paying attention to their smartphones.

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Many research studies have documented high usage of smartphones and the Internet. For example, 92 percent of college students report that they have texted, browsed the web, sent pictures, or visited social networks during class time (Tindell & Bohlander, 2012). By checking college students' phone bills (with their permission!), Judith Gold and coworkers (2015) determined that they send an average of 58 text messages a day, and Rosen and coworkers (2013) showed that during a 15-minute study session, students averaged less than 6 minutes on-task before interrupting studying to stretch, watch TV, access websites, or use technology such as texting or Facebook. What's particularly remarkable is how suddenly this has come upon us. In 2007 only 4 percent of American adults owned smartphones (Radwanick, 2012), but in 2019, just 12 years later, 82 percent of American adults, and 96 percent between the ages of 18 and 29, owned smartphones (Pew Research Center, 2019; Ward et al., 2017).

How often do you consult your phone? If you check your phone constantly, one explanation of your behavior involves **operant conditioning**, a type of learning in which behavior is controlled by rewards (called reinforcements) that follow behaviors (Skinner, 1938). A basic principle of operant conditioning is that the best way to ensure that a behavior will continue is to reinforce it intermittently. So when you check your phone for a message and it's not there, well, there's always a chance it will be there the next time. And when it eventually appears, you've been intermittently reinforced, which strengthens future phone-clicking behavior. Some people's dependence on their phone is captured in the following sticker, marketed by Ephemera, Inc: "After a long weekend without your phone, you learn what's really important in life. Your phone." (See Bosker, 2016, for more on how smartphones are programmed to keep you clicking.)

Constant switching from one activity to another has been described as "continuous partial attention" (Rose, 2010), and here is where the problem lies, because as we saw for driving, distraction from a task impairs performance. It isn't surprising, therefore, that people who text more tend to have lower grades (Barks et al., 2011; Kuznekoff et al., 2015; Kuznekoff & Titsworth, 2013; Lister-Landman et al., 2015), and in extreme cases, some people are "addicted" to the Internet, where addiction is defined as occurring when Internet use negatively affects a number of areas of a person's life (for example, social, academic, emotional, and family) (Shek et al., 2016).

What's the solution? According to Steven Pinker (2010), given that the computer and Internet are here to stay, "the solution is not to bemoan technology, but to develop strategies of self-control, as we do with every other temptation in life." This sounds like good advice, but sometimes powerful temptations are difficult to resist. One example, for some people, is chocolate. Another is checking their phone. So perhaps a solution might be to decide to limit the number of times you consult your phone.

But to make things even more interesting, a recent study has shown that even if you decide not to interact with your phone, its mere presence can have negative effects on memory and intelligence. Adrian Ward and coworkers (2017) demonstrated this in an experiment in which participants took tests designed to measure cognitive functions that depend on attention. Participants were divided into three groups, based on where their smartphone was when they were taking the tests. The "other room" group left their phone and other belongings outside the testing room. The "pocket/bag" group took their belongings into the testing room, but kept their phone where they normally would, usually in their pocket or bag. The "desk" group took only their phones into the testing room and placed it face down on their desk. Participants in all conditions were instructed to turn their phones to silent by turning off the ring and vibrate.

One result of the study is shown in **Figure 6.30**, which shows how participants scored on a test of working memory capacity. Working memory is a memory function that is involved in temporarily holding and manipulating information in the mind while carrying out tasks such as comprehension, solving problems, and reasoning (Baddeley & Hitch, 1974; Goldstein & Brockmole, 2019). These results show that performance in the "desk" and "pocket/bag" conditions were significantly lower than performance in the "other room" condition. Thus, just having the phone within reach caused a decrease in working memory capacity. Ward also showed that having the phone on the desk caused a decrease in scores on a test of intelligence. Based on these results, Ward and coworkers proposed that a potentially costly side effect of the presence of

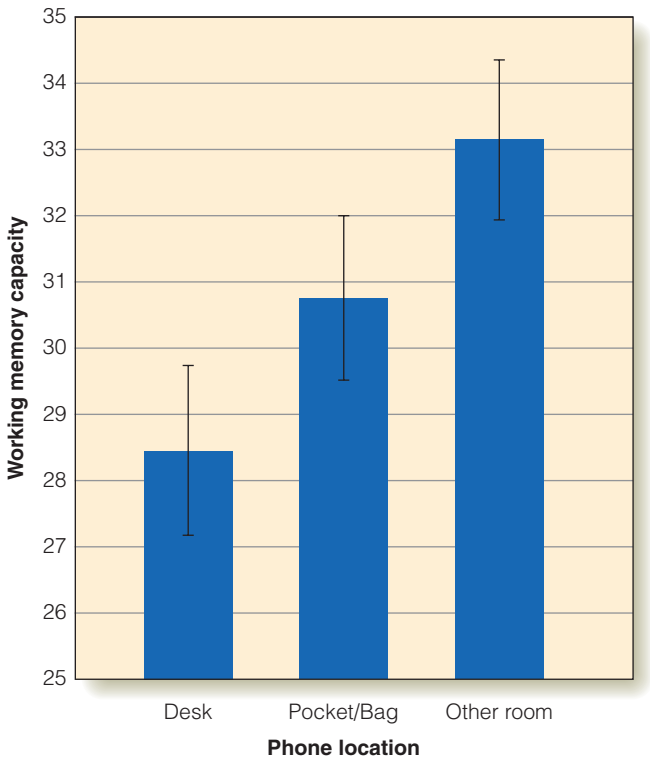

Figure 6.30 How proximity of a smartphone affects working memory capacity. Working memory was lower when the phone was in the same room—either on the desk or in the person's bag or pocket—compared to when it was in the other room. (From Ward et al., 2017)

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smartphones is "smartphone-induced brain drain." They suggest that one way to prevent this brain-drain is "defined and protected periods of separation," similar to the situation in the "other room" group who were physically separated from their phones. This may be easier said than done, but at a minimum it seems unwise to have the phone in plain view on your desk, because it may be draining your attention, even though you think you are ignoring it.

6.9 Disorders of Attention: Spatial Neglect and Extinction

We've seen that when we are paying attention to one thing, we may miss other things. This is a consequence of the fact that we can only focus our attention on one place at a time. But there is a neurological condition called **spatial neglect** that exaggerates this effect.

Consider, for example, the case of Burgess, a 64-year-old male who had a stroke that caused damage to structures in his parietal lobe on the right side of his brain. Burgess became unaware of sounds, people, and objects that were in the left side of his visual field. When he walked down the street, he hugged the right side of the pavement, brushing up against walls and hedges. He didn't notice potential dangers coming from the left, so couldn't go out on his own (Hoffman, 2012).

This ignoring of the side of space opposite the side of the brain damage has been measured in clinical tests. As shown in **Figure 6.31**, spatial neglect patients will (a) draw only the right side of an object when asked to draw it from memory, (b) mark only target circles on the right side of a display, and (c) place a mark far to the right when asked to mark the center of a line. This rightward bias is also reflected in everyday behaviors such as eating food only on the right side of a plate and shaving or grooming only the right side of the face. In other words, people with neglect due to damage to their right hemisphere behave as if the left half of their visual world no longer exists (Driver & Vuillemier, 2001; Harvey & Rossit, 2012).

One conclusion from symptoms such as these might be that the person is blind on the left side of the visual field. This was, in fact, an early explanation of neglect (Bay, 1950). But an experiment by Edoardo Bisiach and Claudio Luzzatti (1978) put an end to that explanation, by asking a patient with neglect to describe things he saw when imagining himself standing at one end of the Piazza del Duomo in Milan, a place with which he had been familiar before his brain was damaged (**Figure 6.32**).

The patient's responses showed that he neglected the left side of his mental image, just as he neglected the left side of his perceptions. Thus, when he imagined himself standing at A, he neglected the left side and named only objects to his right (small a's). When he imagined himself standing at B, he continued to neglect the left side, again naming only objects on his right (small b's). Thus, neglect can occur even if the person is imagining a scene with his or her eyes closed. Other research also showed that patients with visual neglect *do* see things on their left if they are told to pay attention to what's on the left side of the environment. The problem in neglect, therefore, seems to be a lack of *attention* to what's on the left, rather than a loss of *vision* on the left.

A condition that often accompanies neglect, **extinction**, is demonstrated in the laboratory as follows. A patient is told to look at a "fixation cross," so she is always looking straight ahead, and when a light is flashed to her left side, she reports seeing the light. This indicates that she is not blind on her left side. But if two lights are simultaneously flashed, one on the left and one on the right, she reports that she sees a light on the right, but does not report seeing a light on the left. Thus, lack of awareness of what is happening on the left occurs when a competing stimulus is presented on the right.

Extinction provides insight into attentional processing because it suggests that the unawareness of stimuli on the left is caused by competition from the stimuli on the right, with the left ending up being the loser. Thus, when there is a

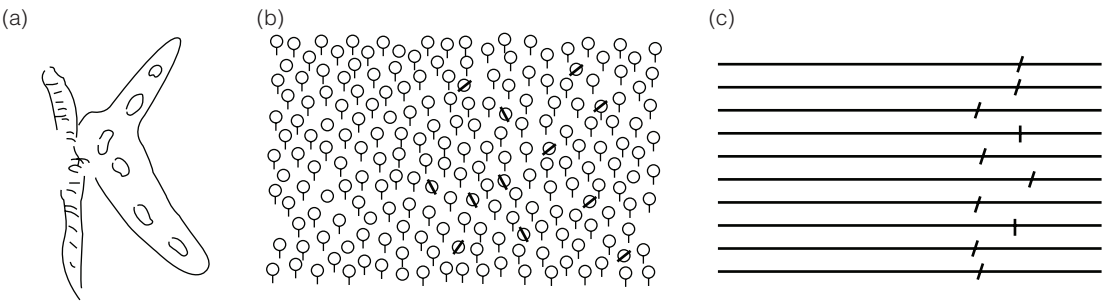

Figure 6.31 Test results for a spatial neglect patient. (a) A starfish drawn from memory is missing its left side; (b) when asked to mark target circles—the ones without a vertical stem—the patient only marked circles on the right; (c) when asked to place a mark at the center of each horizontal line, the mark was placed to the right of center. (From Harvey & Rossit, 2012)

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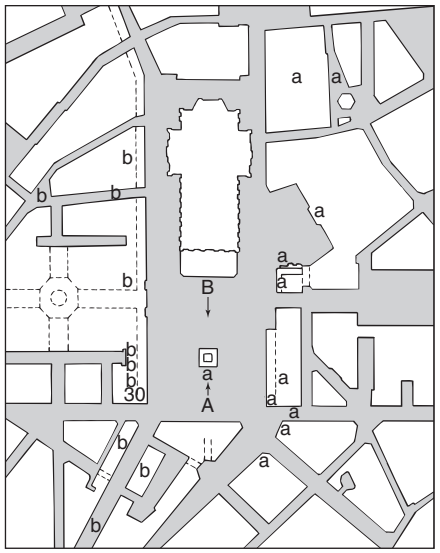

Figure 6.32 Piazza del Duomo in Milan. When Bisiach and Luzzatti's (1978) patient imagined himself standing at A, he could name objects indicated by the a's. When he imagined himself at B, he could name objects indicated by the b's. (Bisiach & Luzzatti, 1978)

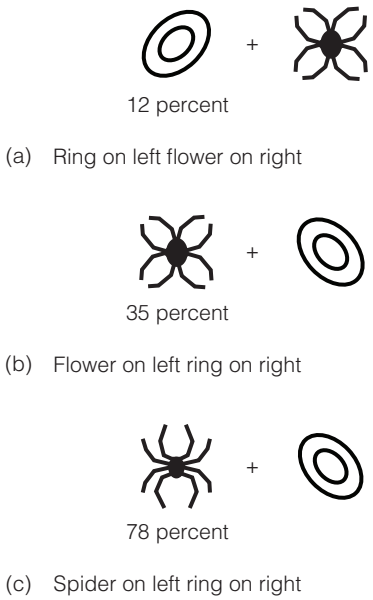

Figure 6.33 A series of tests to determine the degree of extinction for different pairs of stimuli. The number below the left image indicates the percentage of trials on which that image was identified by a patient who usually shows neglect of objects in the left side of the visual field. (a) Ring on left, flower on right; (b) flower on left, ring on right; (c) spider on left, ring on right. (Vuilleumier & Schwartz, 2001, Fig 1b)

stimulus only on the left, the signals generated by this stimulus are transmitted to the brain and the patients see the stimulus. However, when a stimulus is added on the right, the same signal is still generated on the left, but the patient doesn't "see" on the left because attention has been distracted by the more powerful stimulus on the right.

"Seeing" or "conscious awareness" is therefore a combination of signals sent from stimuli to the brain *and* attention toward these stimuli. This happens in non-brain-damaged people as well, who are often unaware of things happening off to the side of where they are paying attention—but there is a difference. Even though they may miss things that are off to the side, they are aware that there is an "off to the side"!

There's still more to learn from the phenomenon of extinction, because it turns out that extinction can be partially eliminated for certain types of stimuli. When a ring stimulus the patient has never seen before is presented on the left and a flower stimulus which also hasn't been previously seen is presented on the right, patients with visual neglect see the ring on only 12 percent of the trials (**Figure 6.33a**) (Treisman & Gelade, 1980; Treisman, 1985). Extinction is therefore high when the ring is on the left. However, when the stimuli are switched so the flower appears on the left, perception rises to 35 percent (**Figure 6.33b**). Finally, when a spider is presented on the left, it is seen on 78 percent of the trials (**Figure 6.33c**) (Vuilleumier & Schwartz, 2001a). In a similar experiment, patients were more likely to see sad or smiley faces on the left than neutral faces (Vuilleumier & Schwartz, 2001b).

Why is the patient more likely to see the spider? The answer seems obvious: the spider attracts attention, perhaps because it is menacing and causes an emotional response, whereas the flower shape does not. But how do patients know that the shape on the left is a spider or a flower? Don't they need to have seen the spider or flower? But if they've seen them, why do they, as in the case of the ring and the flower, often fail to report seeing them?

What apparently is happening is that the flower and spider are processed by the brain at a subconscious level to determine their identity, and then another process determines which stimuli will be selected for conscious vision. The identification at a subconscious level before attention has occurred is an example of **preattentive processing**, which we mentioned at the beginning of the chapter in connection with Anne Treisman's feature integration theory of attention (see page 126). The patient isn't aware of preattentive processing, because it is hidden and happens within a fraction of a second. What the patient is aware of is which stimuli are selected to receive the attention that leads to conscious vision (Rafel, 1994; Vuilleumier & Schwartz, 2001a, 2001b). Thus, neglect and extinction provide more examples of the role of attention in creating our conscious awareness of the environment.

SOMETHING TO CONSIDER:

Focusing Attention by Meditating

Two people are sitting in chairs, feet on the ground, eyes closed. What's going on in their minds? We can't, of course, tell by looking, but we know that they are meditating. What's that all about, and what does it have to do with attention?

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Meditation is an ancient practice that originated in Buddhist and Hindu cultures, which involves different ways of engaging the mind (Basso et al., 2019). In a common form of meditation, called **focused attention meditation**, the person focuses on a specific object, which can be the breath, a sound, a mantra (a syllable, word, or group of words), or a visual stimulus. There are other types of meditation, as well, such as open-monitoring meditation, in which the person observes thoughts, emotions, and sensations as they arise, in a nonjudgmental way, and loving-kindness meditation, in which the person generates thoughts of love, kindness, and empathy toward others and themselves. In the remainder of this section, we will consider focused attention meditation.

Most meditation practice in the United States is focused attention meditation, with the two most popular meditation apps, *Calm* and *Headspace*, emphasizing paying attention to the in and out of the breath. The fact that these apps are multimillion dollar businesses, each with over 1 million paying subscribers, testifies to the growing popularity of meditation, as does the fact that the percentage of adults in the United States who meditated in the last 12 months increased from 4.1 percent in 2012 to 14.2 percent in 2017, which translates into 35 million adults in 2017 (Clarke et al., 2018).

Let's return to our meditators, who we left sitting with their eyes closed. Perhaps the best way to begin describing their experience is to consider what was going on in their minds before they sat down to meditate. One of the characteristics of the mind is that it is very active. Engaging in specific tasks like studying or solving problems involves task-oriented attention. But sometimes this task-oriented attention is interrupted by thoughts that have nothing to do with the task. You may have experienced this if, as you were studying, your mind drifted off to contemplate something that is going to happen later, or something that happened earlier in the day. This type of non-task-oriented mind activity is called day dreaming or **mind wandering**.

Matthew Killingsworth and Daniel Gilbert (2010) determined the prevalence of mind wandering by using a technique called **experience sampling**, based on an iPhone app, which beeped at random times as participants went about their daily lives. When they heard the beep, participants reported that they were mind wandering 47 percent of the time. This scientifically determined result would probably not be surprising to Buddhist meditators, who coined the term "monkey mind" to refer to a mind that is constantly active, often to the detriment of focusing attention on a task or being able to relax without being bothered by all the thoughts created by the pesky monkey mind.

So when our meditators sit down to meditate, their task is to turn off the monkey mind! To accomplish this, they focus their attention on the in and out of their breathing, so their consciousness is centered on "breathing in" and "breathing out." But invariably the monkey mind intrudes, and when the person realizes that they are thinking about something other than their breath they acknowledge the thought, without becoming involved in it, and return their attention to the breath.

Meditation, therefore, involves a cycle of focused attention, an interruption by mind wandering, awareness of the interruption, then focusing attention back on the breath. What this sequence demonstrates is that attention can be used not only to focus on a particular object, place, or activity, as we have been discussing in most of this chapter, but can also be used to "clear the mind" by turning off that sometimes annoying monkey that keeps chattering in our head. As meditators become more practiced, they are able to spend more time in the focused attention part of the cycle (Hasenkamp et al., 2012).

There's an old Zen story about 15th century Zen Master Ikkyu, who, when asked for the source of the highest wisdom answered, "Attention, attention, attention!" (Austin, 2009). What does this mean? It could be applied to the cycle of focusing and shifting attention we have just described. Another interpretation is that we could substitute the word "awareness" for attention (Beck, 1993).

Philosophical discussions about the importance of attention in meditation and life in general aside, there is a great deal of scientific evidence that meditation has many beneficial effects, including pain relief (Zeidan & Vago, 2016), stress reduction (Goyal et al., 2014), improving cognitive functions such as memory (Basso et al., 2019), and, not surprisingly, improving the ability to focus attention (Moor & Malinowski, 2009; Semple, 2010). Other experiments have shown not only that meditation affects behavior, but that it also affects activity in areas of the brain associated with regulation of thought and action (Fox et al., 2016) and causes reorganization of neural networks that extend over large areas of the brain (Tang et al., 2017).

DEVELOPMENTAL DIMENSION Infant Attention and Learning Object Names

How do infants learn the names of objects? The answer to that question is complicated, but an important part of the answer is "by paying attention while interacting with an adult—usually a parent." Another way of stating this is that infants typically learn words with a social partner, who is most often one of their parents. There are two crucial aspects of this interaction. First, the child directs their attention to a particular object. Second, as the child is attending, the parent names the object. Until recently, it has been difficult to study this interaction between attention and naming because of difficulties in measuring exactly where an infant is directing their attention. But this problem has been solved by the development of **head-mounted eye tracking**.

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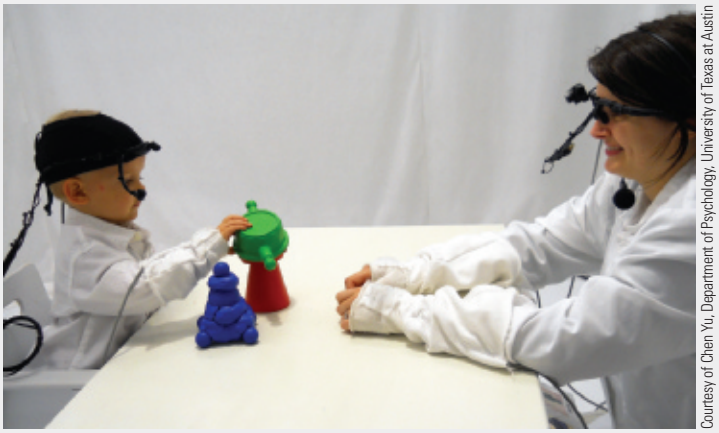
METHOD | Head-Mounted Eye Tracking

Eye tracking has been measured in adults by having them keep their heads steady with the aid of a chin rest, and then tracking their eye movements as they scan a picture of a scene (Figure 6.9). This technique has yielded valuable information about attention, but is both an artificial situation and not feasible for infants.

Head-mounted eye tracking solves the problem of artificiality and suitability for infants by fitting a perceiver with two devices: (1) a head-mounted scene camera, which indicates the orientation of the perceiver's head and their general field of view, and (2) an eye camera, which indicates the precise location where the person is looking within that field of view (Borjon et al., 2018).

Figure 6.34 shows an infant and parent wearing head-mounted eye trackers while playing with toys. **Figure 6.35** shows attention records recorded as an infant and parent looked at three different toys, with purple indicating looking at the partner's face and the other colors indicating attention to each toy. The infant's fixations are on the top record and the parent's records are on the bottom record. The purple in the bottom record indicate that the parent glances often at the infant's face. In contrast, the infant's fixations are focused on the toys.

We can distinguish two different types of infant attention. The black arrows above the infant record indicate the beginnings of periods of *sustained attention*, which is attention to an object lasting 3 seconds or more. The red arrows below the record indicate periods of *joint attention*, which are periods of at least 0.5 seconds when infant and parent are looking at the same object.



Courtesy of Chen Yu, Department of Psychology, University of Texas at Austin

Figure 6.34 Infant and parent wearing head-mounted tracking devices that measure where they are looking while playing with toys. The parent is also wearing a microphone to determine when she is speaking.

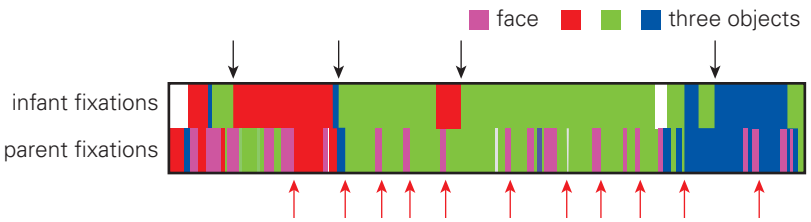


Figure 6.35 How infants and parents directed their attention during toy play. See text for an explanation of this figure. (From Yu et al., 2018)

Chen Yu and coworkers (2018) used head-mounted eye tracking to measure where 9-month-old infants and a parent were directing their attention as they were playing with toys, and the parent's speech was recorded, in order to determine where the infant was looking and when the parent named a toy.

By considering both the looking data and the speech data, Yu identified *high-quality naming events*—instances in which the parent named the object while the infant was looking at it. For each infant, they multiplied the *quality* of naming—the proportion of naming that occurred when the infant was looking at the object—times the *quantity* of naming—the number of times the parent named an object. **Figure 6.36** plots the infant vocabulary at 12 months versus the quality × quantity measure determined at 9 months, with each data point representing an individual infant–parent pair. The wide range in the quality × quantity measure reflects the fact that there were large individual differences in how often the parents named objects, with frequencies ranging from 4.4 to 16.4 naming instances per minute. The relationship between naming and later vocabulary is especially important, because larger early vocabulary is associated with better future language ability and school achievement (Hoff, 2013; Murphy et al., 2014).

The relationship between vocabulary at 12 months and naming at 9 months shown in Figure 6.36 is based on naming that occurred during infant sustained attention—when the infant's attention was focused on an object for 3 seconds or longer. However, when Yu considered naming that occurred when there was no sustained attention, but only joint attention (that is, when the infant and adult were looking at an object at the same time, but the infant's gaze lasted less than 3 seconds), they found that naming did not predict later vocabulary. Thus, the crucial condition for infant name learning is focusing attention on an object for a sustained period of time, and then hearing the object's name.

If word learning doesn't occur when there is only joint attention, does joint attention serve a purpose? Chen Yu and Linda Smith (2016) studied this question by measuring where

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11- to 13-month-old infants and their parents were looking as they played with toys. Yu and Smith found that 65 percent of instances of sustained attention to a toy occurred along with joint attention, that infants' sustained attention was longer when joint attention also occurred, and that longer periods of joint attention were associated with longer sustained attention. The message of these results is that when the parent is demonstrating interest in an object by looking at it, they transmit this interest to the infant by doing other things like talking about the object and touching it, and this encourages the infant to look longer at the object (Suarez-Rivera et al., 2019).

At the beginning of our discussion we stated that infants typically learn with a social partner, usually a parent. But infants rarely look at the parent's face during toy play (Figure 6.35), because what's important to the infant are the toys. Instead, infants learn an object's name (1) by following the cue of the parent's attention, which is indicated by talking about an object and touching it, and (2) by hearing the object's name while their attention is focused on the object.

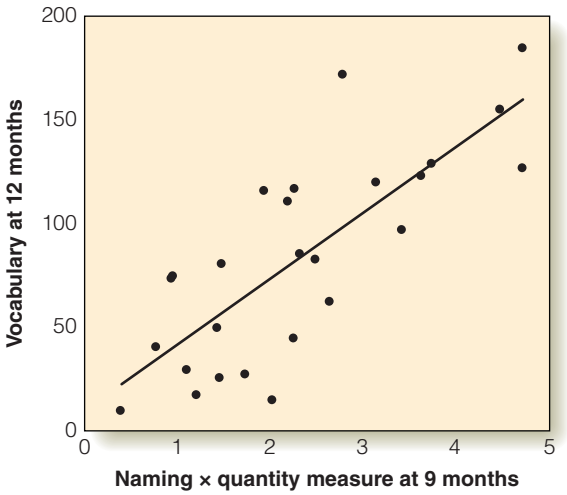

Figure 6.36 The relationship between infant vocabulary at 12 months and the quality of naming measured in the Yu et al. (2018) experiment. See text for details.

TEST YOURSELF 6.2

1. Describe Eagly's experiment that provided evidence for the same-object advantage.
2. Describe Carrasco's experiment that showed an object's appearance can be changed by attention.
3. Describe O'Craven's experiment in which people observed superimposed face and house stimuli. What did this experiment indicate about the effect of attention on the responding of specific brain structures?
4. Describe Datta and DeYoe's experiment on how attending to different locations activates the brain. What is an attention map? What was the point of the "secret place" experiment? Compare this experiment to the "mind reading" experiments described at the end of Chapter 5.
5. Describe Womesdorf and coworkers' experiment in which they recorded from neurons in a monkey's temporal lobe. How did they show how receptive field location is affected by attention?
6. Describe the following two situations that illustrate how not attending can result in not perceiving: (1) inattentional blindness and (2) change detection.
7. What is the evidence that driving while talking on a smartphone or while texting is a bad idea?
8. What is the evidence that high usage of smartphones and the Internet can, under some conditions, have negative effects on performance?
9. Describe the experiment that showed that just having your smartphone nearby can affect scores on tests of memory and intelligence.
10. What is spatial neglect? What causes it? Describe the experiment that showed that neglect to stimuli on the left isn't due to being blind on the left.
11. What is extinction? What does the "spider" experiment demonstrate about conscious and unconscious attentional processing?
12. What is the connection between meditation and attention?
13. Describe how head-mounted eye tracking was used by Yu and coworkers (2018) to measure the attention of infants and their parents as they were playing with toys. What is the conclusion from this research?

THINK ABOUT IT

1. If salience is determined by characteristics of a scene such as contrast, color, and orientation, why might it be correct to say that paying attention to an object can increase its salience? (p. 134)
2. How is the idea of regularities of the environment that we introduced in Chapter 5 (see page 105) related to the cognitive factors that determine where people look? (p. 131)
3. Can you think of situations from your experience that are similar to the change detection experiments in that you missed seeing an object that became easy to see once you knew it was there? What do you think was behind your initial failure to see this object? (p. 137)

Hint for change detection demonstration on page 138: Pay attention to the sign near the lower left portion of the picture.

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KEY TERMS

Attention (p. 124)
Attentional capture (p. 130)
Binding (p. 126)
Change blindness (p. 138)
Cocktail party effect (p. 124)
Comparator (p. 128)
Conjunction search (p. 126)
Continuity error (p. 138)
Corollary discharge signal (CDS) (p. 128)
Corollary discharge theory (p. 128)
Covert attention (p. 124)
Dichotic listening (p. 124)
Experience sampling (p. 143)
Extinction (p. 141)
Feature integration theory (FIT) (p. 126)
Feature search (p. 126)
Fixation (p. 128)
Focused attention meditation (p. 143)
Focused attention stage (p. 126)
Head-mounted eye tracking (p. 143)
Illusory conjunction (p. 126)
Image displacement signal (IDS) (p. 128)
Inattentional blindness (p. 136)
Meditation (p. 143)
Mind wandering (p. 143)
Motor signal (MS) (p. 128)
Operant conditioning (p. 140)
Overt attention (p. 124)
Perceived contrast (p. 134)
Preattentive processing (p. 142)
Preattentive stage (p. 126)
Precueing (p. 125)
Predictive remapping of attention (p. 130)
Saccadic eye movement (p. 128)
Saliency map (p. 130)
Same-object advantage (p. 134)
Scene schemas (p. 131)
Selective attention (p. 124)
Shadowing (p. 124)
Spatial attention (p. 125)
Spatial neglect (p. 141)
Visual salience (p. 130)
Visual search (p. 126)

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How did McKayla Maroney of the U.S. gymnastics team, vaulting at the 2012 London Olympics, get into this position, and then execute a landing just moments later? The answer involves a close connection between perception and action, which also occurs for everyday actions such as walking across campus or reaching across a table to pick up a cup of coffee.

EMPICS Sport - EMPICS/Getty Images

Learning Objectives

After studying this chapter, you will be able to ...

- Understand the ecological approach to perception.
- Describe the information people use to find their way when walking and driving.
- Understand how the brain's "GPS" system creates cortical maps that help animals and people find their way.
- Describe how carrying out simple physical actions depends on interactions between the sensory and motor components of the nervous system, combined with prediction.
- Understand the physiology behind our ability to understand other people's actions.
- Understand what is behind the idea that the purpose of perception is to enable us to interact with the environment.
- Understand what it means to say that "prediction is everywhere."
- Describe what an infant affordance is and how research has studied this phenomenon

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CHAPTER 7

Taking Action

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Reacting to Information Created by Movement
The Senses Work Together
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Individual Differences in Wayfinding
TEST YOURSELF 7.1

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7.5 Observing Other People's Actions
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7.6 Action-Based Accounts of Perception

SOMETHING TO CONSIDER: Prediction Is Everywhere

DEVELOPMENTAL DIMENSION: Infant Affordances

TEST YOURSELF 7.2

THINK ABOUT IT

Some Questions We Will Consider:

- What is the connection between perceiving and moving through the environment? (p. 149)
- How do we find our way from one place to another? (p. 154)
- How do sensory and motor functions interact as we reach for a bottle of ketchup? (p. 160)
- How do neurons in the brain respond when a person performs an action and when the person watches someone else carry out the same action? (p. 164)

What does "action" have to do with perception? One perspective on this question is provided by the sea squirt, a tadpole-like creature with a spinal cord connected to a primitive brain, an eye, and a tail, which helps it find its way as it swims through the water (**Figure 7.1a**). However, early in its life, the sea squirt gives up its traveling ways and finds a place like a rock, the ocean floor, or the hull of a ship to attach itself (**Figure 7.1b**). Once the sea squirt finds the place where it will remain for the rest of its life, it has no more use for its eye, brain, or flipping tail, and so absorbs its brain and eye into its body (Beilock, 2012).

The message of the sea squirt is that once it becomes totally stationary, it doesn't have any use for the perceptual capacities provided by the brain. We can appreciate what this has to do with human perception by noting that in most of the early research on perception, human participants were much like sea squirts—attached firmly to their chairs, responding to stimuli or scenes on a computer screen. Drawing an analogy between brainless sea squirts and participants in perception experiments might be going a bit far, but the fact is that people, in contrast to mature sea squirts, are in almost constant motion while awake and one of the purposes of their brains is to enable them to act within the environment. In fact, Paul Cisek and John Kalaska (2010) state that the primary purpose of the brain is "to endow organisms with the ability to adaptively interact with the environment."

So to understand perception we need to take a step beyond our discussion in the previous chapter, when we described how people direct their attention to specific objects or areas in the environment, and broaden our perspective to consider the interaction between perception and our ability to interact with the environment.

So what does this interaction look like? Let's consider the situation when you have just left class and are heading to the student union for lunch. That isn't much of a problem, because you know your way around campus. But that's something you learned as you created the campus map in your head. So now, having consulted your mental map, how do you stay

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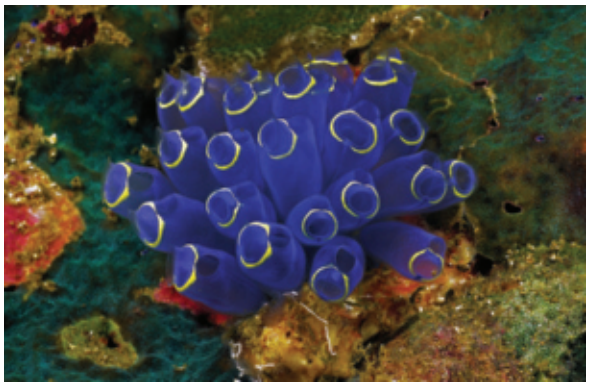
Wim Van Egmond/Science Source

(a) Top: Sea squirt tadpole



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(b) Adult sea squirts attached to a rock

Figure 7.1 (a) A swimming sea squirt. Its spinal cord is attached to a primitive brain, and it has eyes. (b) A number of mature sea squirts attached to a rock. The spinal cord, brain, and eyes are gone.

on course during your trip? This may seem like a simple question, because you do this without thinking when in a familiar environment. But, as we will see, perception and memory play an important role in keeping us on course.

Another interaction with the environment occurs as you are eating lunch. You reach across the table, pick up your drink, and raise it to your lips. Another thing you do without much thinking or effort, but which involves complex interactions between perception and taking action. This chapter looks at how perception operates as we move through and interact with the environment. To begin, we go back in history to consider the ideas of J. J. Gibson, who championed the *ecological approach to perception*.

7.1 The Ecological Approach to Perception

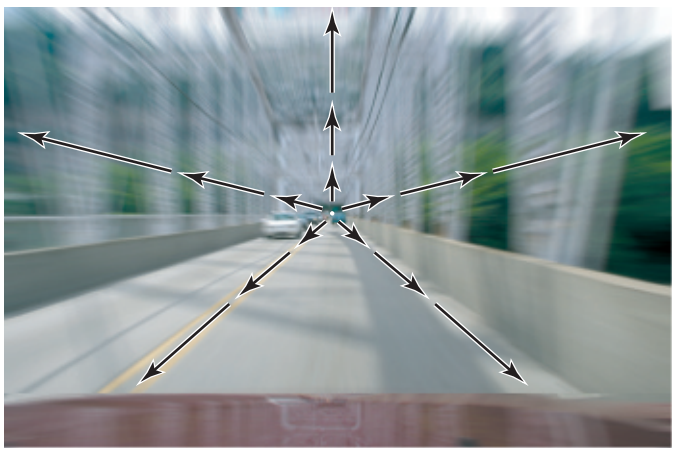
Through most of the 20th century, the dominant way perception research was carried out was by having stationary observers look at static stimuli in the laboratory. However, in the 1970s and 1980s, one group of psychologists, led by J. J. Gibson, argued that this traditional way of studying perception was flawed because placing participants in small testing rooms to look at simple stimuli ignores what a person perceives when he or she performs natural, real-world tasks like walking down a street or drinking a glass of water. Perception, Gibson argued, evolved so that we can move within, and act upon, the world; therefore, he thought a better approach was to study perception in situations where people move through and interact with the environment. Gibson's approach, which focused on perception in natural contexts, is called the **ecological approach to perception** (Gibson, 1950, 1962, 1979). One goal of the ecological approach is to determine how movement creates perceptual information that helps people move within the environment.

The Moving Observer Creates Information in the Environment

To understand what it means to say that movement creates perceptual information, imagine that you are driving down an empty street. No other cars or people are visible, so everything around you—buildings, trees, traffic signals—is stationary. Even though the objects around you aren't moving, your movement *relative to the objects* causes you to see the houses and trees moving past when you look out of the side window. And when you look at the road ahead, you see the road moving toward you. As your car hurtles forward when crossing a bridge, everything around you—the sides and top of the bridge, the road below—moves past you in a direction opposite to the direction you are moving (**Figure 7.2**).

The movement described above, in which movement of an observer creates movement of objects and the scene relative to the observer, is called **optic flow**. Optic flow has two important characteristics:

1. Optic flow is more rapid near the moving observer, as shown in Figure 7.2 by longer arrows indicating more rapid flow. The different speed of flow—fast near the observer and slower farther away—is called the **gradient**



Barbara Goldstein

Figure 7.2 The side and top of the bridge and the road below appear to move toward a car that is moving forward. This movement is called *optic flow*.

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of flow. The gradient of flow provides information about how fast the observer is moving. According to Gibson, the observer uses the information provided by the gradient of flow to determine his or her speed of movement.

2. There is no flow at the destination toward which the observer is moving. The absence of flow at the destination point is called the **focus of expansion (FOE)**. In Figure 7.2 the FOE, marked by the small white dot, is at the end of the bridge; it indicates where the car will end up if its course is not changed.

Another important concept of the ecological approach is the idea of **invariant information**—information that remains constant regardless of what the observer is doing or how the observer is moving. Optic flow provides invariant information because the same flow information is present each time the observer is moving through the environment in a particular way. For example, the FOE always occurs at the point toward which the observer is moving. If an observer changes direction, objects in the scene may change, but there is still a FOE. Thus, even when specific aspects of a scene change, optic flow and the FOE continue to provide information about how fast a person is moving and where he or she is heading. When we consider depth perception in Chapter 10, we will see that Gibson proposed other sources of invariant information, which indicate an object's size and its distance from the observer.

Reacting to Information Created by Movement

After identifying information created by the moving observer, the next step is to determine whether people use this information. Research on whether people use optic flow information has asked observers to make judgments regarding where they are heading based on computer-generated displays of moving dots that create optic flow stimuli. The observer's task is to judge, based on optic flow stimuli, where he or she would be heading relative to a reference point. Examples of these stimuli are depicted in **Figures 7.3a** and **7.3b**. In each figure, the lines represent the movement trajectories of individual dots. Longer lines indicate faster movement (as in Figure 7.2). Depending on the trajectory and speed of the dots, different flow patterns can be created. The flow in Figure 7.3a indicates movement directly toward the vertical line on the horizon; the flow in Figure 7.3b indicates movement to the right of the vertical line. Observers viewing stimuli such as this can judge where they are heading relative to the vertical line to within about 0.5 to 1 degree (Warren, 1995, 2004; also see Fortenbaugh et al., 2006; Li et al., 2006).

Figure 7.4 indicates how movement creates information which, in turn, is used to guide further movement. For example, when a person is driving down the street, movement of the car provides optic flow information, and the observer then uses this flow information to help steer the car. A different example of movement that creates information that is then used to guide further movement is provided by somersaulting.

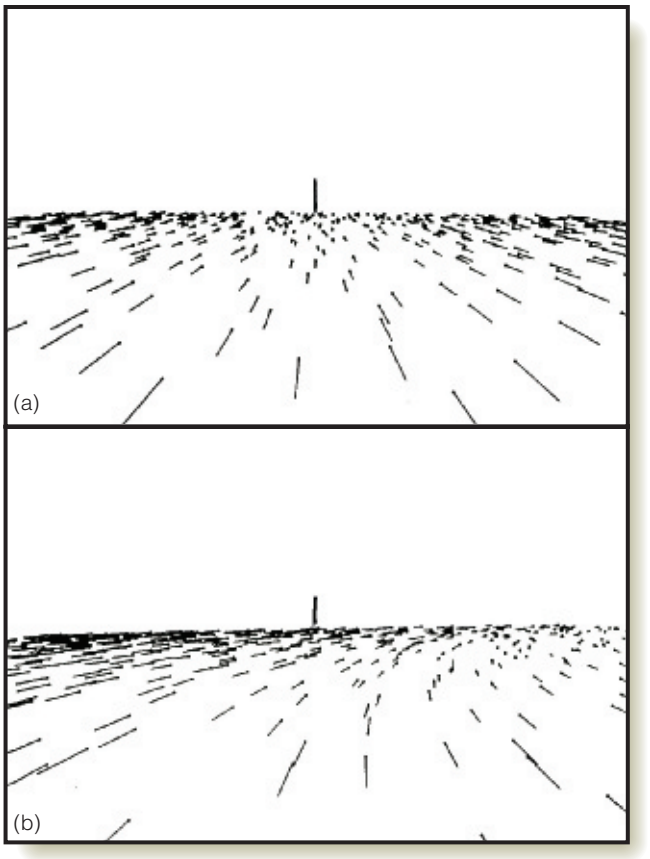

Figure 7.3 (a) Optic flow generated by a person moving straight ahead toward the vertical line on the horizon. The lengths of the lines indicate the person's speed. (b) Optic flow generated by a person moving in a curved path that is headed to the right of the vertical line. (From Warren, 1995)

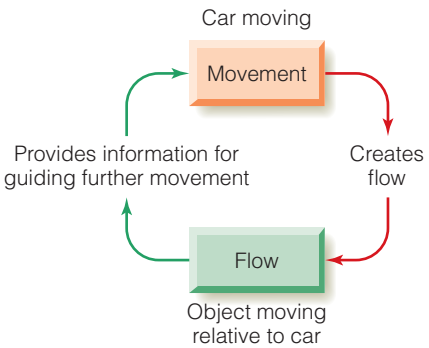

Figure 7.4 The relationship between movement and flow is reciprocal, with movement causing flow and flow guiding movement. This is the basic principle behind much of our interaction with the environment.

We can appreciate the problem facing a gymnast who wants to execute an airborne backward somersault (or backflip) by realizing that, within 600 ms, the gymnast must execute the somersault and then end in exactly the correct body configuration precisely at the moment that he or she hits the ground (**Figure 7.5**). One way this could be accomplished is to learn to run a predetermined sequence of motions within a specific

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Figure 7.5 "Snapshots" of a somersault, or backflip, starting on the left and finishing on the right. (From Bardy & Laurent, 1998)

period of time. In this case, performance should be the same with eyes open or closed. However, Benoit Bardy and Makel Laurent (1998) found that expert gymnasts performed somersaults more poorly with their eyes closed. Films showed that when their eyes were open, the gymnasts appeared to be making in-the-air corrections to their trajectory. For example, a gymnast who initiated the extension of his or her body a little too late compensated by performing the rest of the movement more rapidly. Thus, somersaulting, like driving a car, involves using information created by movement to guide further movement.

The Senses Work Together

Another of Gibson's ideas was that the senses do not work in isolation. He felt that rather than considering vision, hearing, touch, smell, and taste as separated senses, we should consider how each one provides information for the same behaviors. One example of how a behavior originally thought to be the exclusive responsibility of one sense is also served by another one is the sense of balance.

Your ability to stand up straight, and to keep your balance while standing still or walking, depends on systems that enable you to sense the movement and position of your body relative to gravity. These systems include the vestibular canals of your inner ear and receptors in the joints and muscles. However, Gibson (and others) noted that information provided by vision also plays a role in keeping our balance, a fact we can use to emphasize the way the senses work together. One way to illustrate the role of vision in balance is to consider what happens when visual information isn't available, as in the following demonstration.

DEMONSTRATION | Keeping Your Balance

Keeping your balance is something you probably take for granted. Stand up. Raise one foot from the ground and stay balanced on the other. Then close your eyes and notice what happens.

Did staying balanced become more difficult when you closed your eyes? This occurs because vision provides a frame of reference that helps the muscles constantly make adjustments to help maintain balance (Aartolahti et al., 2013; Hallemans et al., 2010; Lord & Menz, 2000).

The importance of a visual frame of reference for balance has also been examined by considering what happens to a person when his or her visual and vestibular senses provide conflicting information regarding posture. For example, David Lee and Eric Aronson (1974) placed 13- to 16-month-old toddlers in a "swinging room" (**Figure 7.6**). In this room, the floor was stationary, but the walls and ceiling could swing toward and away from the toddler. **Figure 7.6a** shows the room swaying toward the toddler. This movement of the wall creates the optic flow pattern on the right. Notice that this pattern is similar to the optic flow that occurs when moving forward, as when driving across the bridge in Figure 7.2.

The optic flow pattern that the toddler observes creates the impression that he or she is swaying forward. After all, the only natural circumstance in which the entire world suddenly moves toward you is a situation in which you are moving (or falling) forward. This perception causes the toddler to sway back to compensate (**Figure 7.6b**). When the room moves back, as in **Figure 7.6c**, the optic flow pattern creates the impression of swaying backward, so the toddler sways forward to compensate. In Lee and Aronson's experiment, although a few of the toddlers were unaffected by the sway, 26 percent swayed, 23 percent staggered, and 33 percent fell down, even though the floor remained stationary throughout the entire experiment!

Even adults were affected by the swinging room. Lee describes their behavior as follows: "oscillating the experimental room through as little as 6 mm caused adult participants to sway approximately in phase with this movement. The participants were like puppets visually hooked to their surroundings and were unaware of the real cause of their disturbance" (p. 173). Adults who didn't brace themselves could, like the toddlers, be knocked over by their perception of the moving room. The swinging room experiments therefore show that vision can override the traditional sources of balance information provided by the inner ear and the receptors in the muscles and joints (also see Fox, 1990; Stoffregen et al., 1999; Warren et al., 1996).

Affordances: What Objects Are Used For

Gibson's emphasis on understanding perception in natural environments extended to how people interact with objects. In connection with this, Gibson introduced the concept of affordances—information that indicates how an object can be used. In Gibson's (1979) words, "The affordances of the environment are what it *offers* the animal, what it *provides for* or *furnishes*." A chair, or anything that is sit-on-able, affords sitting; an object of the right size and shape to be grabbed by a person's hand affords grasping; and so on.

What this means is that perception of an object includes not only its physical properties, such as shape, size, color, and orientation, that enable us to recognize the object, but also

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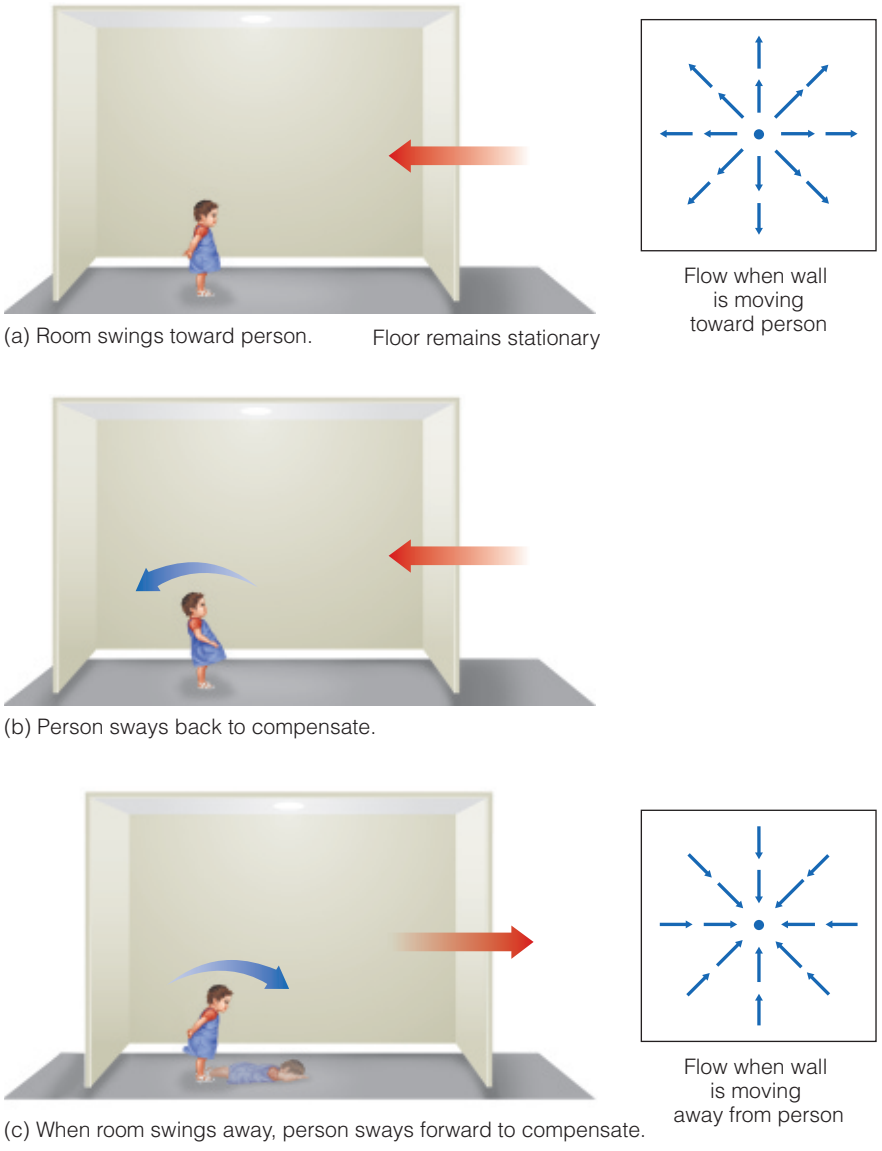
(a) Room swings toward person.
Floor remains stationary
Flow when wall is moving toward person
(b) Person sways back to compensate.
(c) When room swings away, person sways forward to compensate.
Flow when wall is moving away from person

Figure 7.6 Lee and Aronson's swinging room. (a) Moving the room toward the observer creates an optic flow pattern associated with moving forward, so (b) the observer sways backward to compensate. (c) As the room moves away from the observer, flow corresponds to moving backward, so the person leans forward to compensate and may even lose his or her balance. (Based on Lee & Aronson, 1974)

information about how the object is or could be used. For example, when you look at a cup, you might see that it is "a round white coffee cup, about 5 inches high, with a handle," but your perceptual system would also respond with information indicating that it "can be picked up," "can be filled with liquid," or even "can be thrown." Affordances thus go beyond simply recognizing the cup; they guide our interactions with it. Another way of saying this is that "potential for action" is part of our perception of an object.

Gibson's emphasis on (1) studying the acting observer, (2) identifying invariant information in the environment that observers use for perception, (3) considering the senses as working together, and (4) focusing on object affordances was revolutionary for its time. But even though perception researchers were aware of Gibson's ideas, most research continued in the traditional way—testing stationary participants looking at stimuli in laboratory settings. Of course, there is nothing wrong with testing stationary observers in the laboratory, and much of the research described in this book takes this approach. However, Gibson's idea that perception should also be studied as it is often experienced, by observers who are moving and in more naturalistic settings, finally began to take hold in the 1980s, and today perception in naturalistic settings is one of the major themes of perception research.

One modern approach to affordances has looked at the behavior of people with brain damage. Glyn Humphreys and Jane Riddoch (2001) studied affordances by testing patient M.P., who had damage to his temporal lobe that impaired his ability to name objects. M.P. was given a cue, either (1) the name of an object ("cup") or (2) an indication of the object's function ("an item you could drink from"). He was then shown 10 different objects and was told to press a key as soon as he found an object that matched the cue. M.P. identified the object more accurately and rapidly when given the cue that referred to the object's function. Humphreys and Riddoch concluded from this result that M.P. was using his knowledge of an object's affordances to help him identify it.

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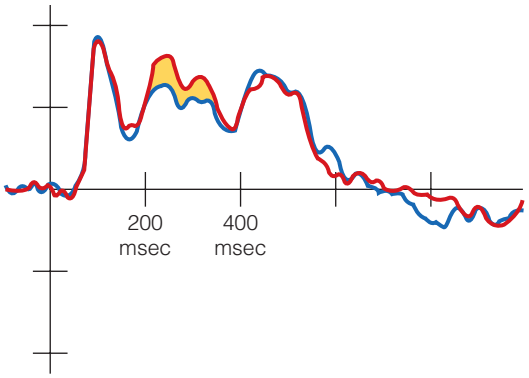

Figure 7.7 EEG response to tools (red) and non-tools (blue), showing that the response to tools is larger between 210 and 270 msecs after they are presented. (From Proverbio, 2011)

Another modern approach has recorded the brain's response to objects. Alice Proverbio and coworkers (2011) recorded a person's electroencephalogram (EEG), which is recorded with electrodes on the scalp that pick up the response of the thousands of neurons under the electrodes. As they were recording the EEG, the person looked at 150 pictures of manipulable tools, 150 pictures of non-tool objects, and 25 pictures of plants. Their task was to respond to the plants by pressing a key and to ignore the other pictures. **Figure 7.7** compares the response to the tools (red) and non-tools (blue), and shows that between 210 and 270 msec after presentation, the tools generated a larger response than the non-tools. They call this response an action affordance because it involves both the object's affordance (what it is for, for example, "pounding" for a hammer) and the action associated with it (the grip necessary to hold the hammer and the movements when pounding in a nail).

The remainder of this chapter focuses on research that considers the following situations in which perception and action occur together in the environment: (1) walking or driving through the environment; (2) finding one's way from one location to another; (3) reaching out and grasping objects; and (4) watching other people take action.

7.2 Staying on Course: Walking and Driving

Following in Gibson's footsteps, a number of researchers have considered the types of information that people use when they are walking or driving. Perceptual information we have already discussed such as optic flow is important, but other sources of information come into play as well.

Walking

How does a person stay on course as he or she is walking toward a specific location? We have already discussed how optic flow can provide invariant information regarding a person's trajectory and speed, but other information can

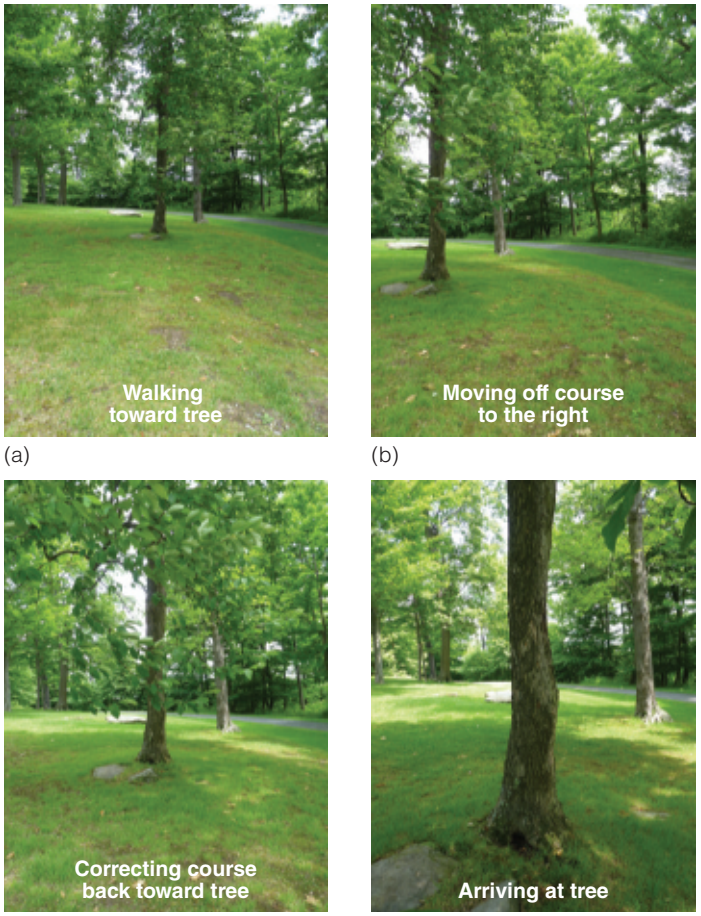

Figure 7.8 (a) As long as a person is moving toward the tree, it remains in the center of the person's field of view. (b) When the person walks off course, the tree drifts to the side. (c) When the person corrects the course, the tree moves back to the center of the field of view, until (d) the person arrives at the tree.

be used as well. For example, when using the visual direction strategy, people keep their body pointed toward their goal. This is shown in **Figure 7.8**, in which the goal is a tree (**Figure 7.8a**). Walking off course causes the tree to drift to the side (**Figure 7.8b**), so a course correction is needed to bring the tree back to the center (**Figures 7.8c and 7.8d**) (Fajen & Warren, 2003; Rushton et al., 1998).

Another indication that optic flow information is not always necessary for navigation is that we can find our way even when flow information is minimal, such as at night or in a snowstorm (Harris & Rogers, 1999). Jack Loomis and coworkers (1992; Philbeck et al., 1997) have demonstrated this by eliminating optic flow altogether, using a "blind walking" procedure in which people observe a target object located up to 12 meters away, then walk to the target with their eyes closed.

These experiments show that people are able to walk directly toward the target and stop within a fraction of a meter of it. In fact, people can do this even when they are asked to walk off in the wrong direction first and then make a turn and walk to the target, all while keeping their eyes

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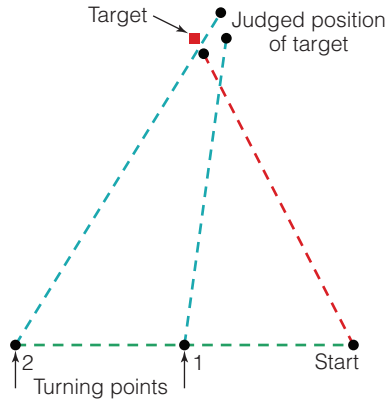

Figure 7.9 The results of a "blind walking" experiment (Philbeck et al., 1997). Participants looked at the target, which was 6 meters from the starting point, then closed their eyes and begin walking to the left. They turned either at point 1 or point 2, keeping their eyes closed the whole time, and continued walking until they thought they had reached the target.

closed. Some records from these "angled" walks are shown in **Figure 7.9**, which shows the paths taken when a person first walked to the left from the starting position and then was told to turn either at point 1 or 2 and walk to a target that was 6 meters away. The fact that the person generally stopped close to the target shows that we are able to navigate short distances accurately in the absence of any visual stimulation at all (also see Sun et al., 2004). Participants in the blind walking experiment accomplished this feat by mentally combining knowledge of their own movements (e.g., muscle movements can give the walker a sense of his or her speed as well as shifts in direction) with their memory for the position of the target throughout their walk. The process by which people and animals keep track of their position within a surrounding environment while they move is called spatial updating (see Wang, 2003).

But just because people can walk toward objects and locations without optic flow information doesn't mean that they don't use such information to help them when it is available. Optic flow provides important information about direction and speed when walking (Durgin & Gigone, 2007), and this information can be combined with the visual direction strategy and spatial updating processes to guide walking behaviors (Turano et al., 2005; Warren et al., 2001).

Driving a Car

Another common activity that requires people to keep track of their movement through the environment is driving. To study information people use to stay on course when driving, Michael Land and David Lee (1994) fitted an automobile in the United Kingdom with instruments to record the angle of the steering wheel and the car's speed, and measured where the driver was looking with a video eye tracker. As we noted earlier, according to Gibson, the focus of expansion (FOE) provides information about the place toward which a moving observer is headed. However, Land and Lee found that although drivers look straight ahead while driving, they tend to look at a spot closer to the front of the car rather than directly at the FOE, which is further down the road (**Figure 7.10a**).

Land and Lee also found that drivers don't use the FOE on curved roads, because the FOE keeps changing as the car rounds the curve, making the FOE a poor indicator of how the car should be steered. When going around a curve, drivers don't look directly at the road, but instead look at the tangent point of the curve on the side of the road, as shown in **Figure 7.10b**. This allows drivers to constantly note the position of the car relative to the lines at the side of the road. By maintaining a constant distance between the car and the lines on the road, a driver can keep the car headed in the right direction (see Kandel et al., 2009; Land & Horwood, 1995; Macuga et al., 2019; Rushton & Salvucci, 2001; Wilkie & Wann, 2003).

7.3 Finding Your Way Through the Environment

In the last section we considered information in the immediate environment that helps walkers and drivers stay on course as they walk toward a goal or drive along a road. But we often travel to more distant destinations that aren't visible from our starting point, such as when we walk across campus from one class to another or drive to a destination several miles away. This kind of navigation, in which we take a route that usually involves making turns, is called wayfinding.

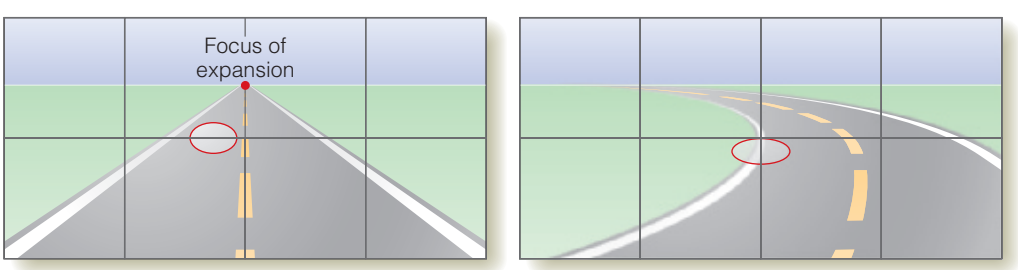

Figure 7.10 Results of Land and Lee's (1994) experiment. Because this study was conducted in the United Kingdom, subjects were driving on the left side of the road. The ellipses indicate the place where the drivers were most likely to look while driving down (a) a straight road and (b) a curve to the left.

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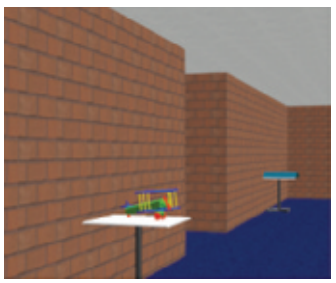
The Importance of Landmarks

One important source of information for wayfinding is landmarks—objects on the route that serve as cues to indicate where to turn. Sahar Hamid and coworkers (2010) studied how participants used landmarks as they learned to navigate through a maze-like environment displayed on a computer screen in which pictures of common objects served as landmarks. Participants first navigated through the maze until they learned its layout (training phase) and then were told to travel from one location in the maze to the other (testing phase). During both the training and testing phases, participants' eye movements were measured using a head-mounted eye tracker like the one in Chapter 6 in which eye movements were measured as a person made a peanut butter and jelly sandwich (see page 132). This maze contained both *decision-point landmarks*—objects at corners where the participant had to decide which direction to turn—and *non-decision-point landmarks*—objects located in the middle of corridors that provided no critical information about how to navigate.

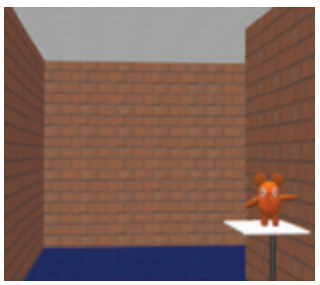
Measurement of the participants' eye movements as they were navigating the maze showed that they spent more time looking at landmarks at decision points, corners where it was necessary to determine which way to turn, than landmarks in the middle of corridors. When maze performance was tested with half of the landmarks removed, removing landmarks that had been viewed less (which were likely to be in the middle of the corridors) had little effect on performance (**Figure 7.11a**). However, removing landmarks that observers had looked at longer caused a substantial drop in performance (**Figure 7.11b**). It makes sense that landmarks that are looked at the most would be the ones that are used to guide navigation, and it has also been found that decision-point landmarks are also more likely to be remembered (Miller & Carlson, 2011; Schinazi & Epstein, 2010).

Hamid's study used behavioral measures to study how landmarks influence wayfinding. But what is happening in the brain? Gabriele Janzen and Miranda van Turennout (2004) studied this question by having participants view a film sequence that moved through a computer-simulated museum (**Figure 7.12**). Decision-point objects marked places where it was necessary to make a turn (**Figure 7.12a**). Non-decision-point objects were located at places where a decision was not required (**Figure 7.12b**).

After studying the museum's layout in the film, participants were given a recognition test while in an fMRI scanner. **Figure 7.12c** indicates activity in an area of the brain known to be associated with navigation called the parahippocampal gyrus (see Figure 4.31, page 85). The left pair of bars indicates that for objects that were remembered, activation was greater for decision-point objects than for non-decision-point objects. But the most interesting



(a) Toy at decision point



(b) Toy at non-decision point

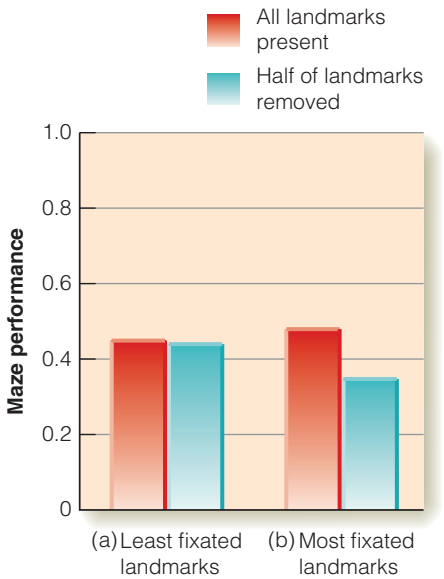
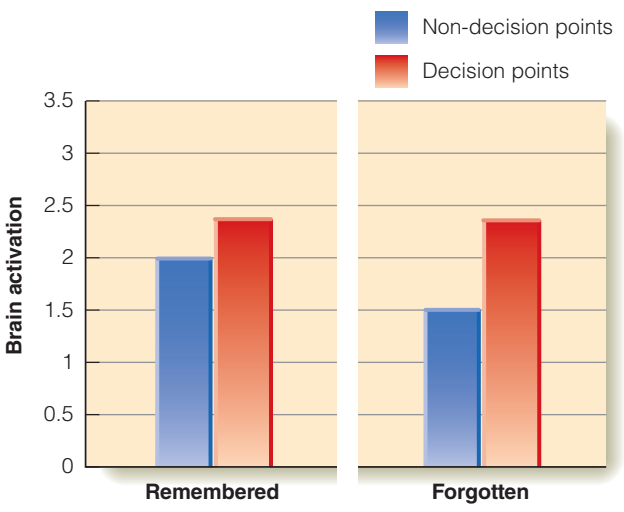


Figure 7.11 Effect of removing landmarks on maze performance. Red = all landmarks are present; blue = half have been removed. (a) Removing half of the least fixated landmarks has no effect on performance. (b) Removing half of the most fixated landmarks causes a decrease in performance. (From Hamid et al., 2010)



(c)

Figure 7.12 (a & b) Two locations in the "virtual museum" viewed by Janzen and van Turennout's (2004) observers. (c) Brain activation during the recognition test for objects that had been located at decision points (red bars) and non-decision points (blue bars). Notice that brain activation was greater for decision-point objects even if they weren't remembered. (Adapted from Janzen & van Turennout, 2004)

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result, indicated by the right pair of bars, is that the advantage for decision-point objects also occurred for objects that were not remembered during the recognition test.

Janzen and van Turennout concluded that the brain automatically distinguishes objects that are used as landmarks to guide navigation. The brain therefore responds not just to the object but also to how relevant that object is for guiding navigation. This means that the next time you are trying to find your way along a route that you have traveled before but aren't totally confident about, activity in your parahippocampal gyrus may automatically be "highlighting" landmarks that indicate when you should continue going straight, turn right, or turn left, even when you may not remember having seen these landmarks before (see also Janzen, 2006; Janzen et al., 2008). In addition to evidence that the brain contains neurons that keep track of landmarks, there is also evidence that the brain creates a map of the environment.

Cognitive Maps: The Brain's "GPS"

Have you ever had the experience of being unsure of where you are, such as emerging from a subway station and not knowing which direction you are facing, or losing track of where you are in a walk in the woods? Joshua Julian and coworkers (2018) suggest that the experience of being lost underscores the fact that we are spatially oriented most of the time—but not always. The idea that we usually know where we are in space has given rise to the idea that we have a map in our heads, called a **cognitive map**, that helps us keep track of where we are.

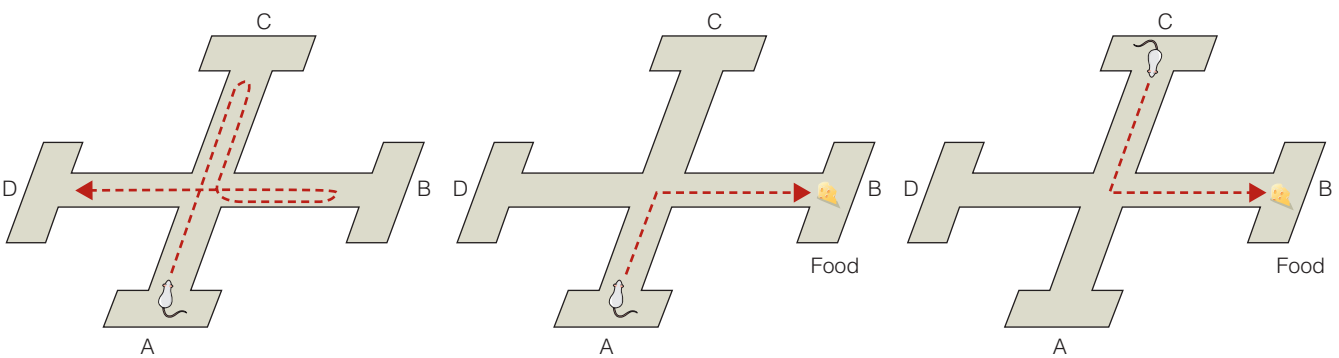
Early research on cognitive maps was carried out by Edward Tolman, who was studying how rats learned to run through mazes to find rewards. In one of his experiments, Tolman (1938) placed a rat in a maze like the one in **Figure 7.13**. Initially, the rat explored the maze, running up and down each of the alleys (**Figure 7.13a**). After this initial period of exploration, the rat was placed at A and food was placed at B, and the rat quickly learned to turn right at the intersection to obtain the food (**Figure 7.13b**). According to simple learning theories of the time, rewarding the rat with food every time it turns right should strengthen the "turn right" response, and so increase the chances that the rat will turn right to obtain food in future.

However, after taking precautions to be sure the rat couldn't determine the location of the food based on smell, Tolman placed the rat at C, and something interesting happened. The rat turned *left* at the intersection to reach the food at B (**Figure 7.13c**). This result is important because it shows that the rat did not merely learn a sequence of moves to a get to the food during training. Instead, the rat was able to use its cognitive map of the spatial layout of the maze to locate the food (Tolman, 1948).

More than 30 years after Tolman's experiments, John O'Keefe recorded the activity of individual neurons in a rat's hippocampus (see Figure 4.31), and found neurons that fired when the rat was in a specific place within the box and that different neurons preferred different locations (O'Keefe & Dostrovsky, 1971; O'Keefe & Nadel, 1978). A record similar to those determined by O'Keefe is shown in **Figure 7.14a**. The gray lines show the path taken by a rat as it wandered around a recording box. Overlaid on top of this path are the locations where four different neurons fired. In this example, the "purple neuron" only fired when the animal was in the upper right portion of the box, and the "red neuron" only fired when the rat was in the lower left corner. These neurons have come to be called **place cells** because they only fire when an animal is in a certain place in the environment. The area of the environment within which a place cell fires is called its **place field**.

The discovery of place cells was an important first step in determining how the brain's "GPS system" works. Further research identified neurons called **grid cells** in an area near the hippocampus called the entorhinal cortex (see Figure 4.31, page 85) which are arranged in regular, gridlike patterns like the three types of grid cells (denoted by orange, blue, and green dots) shown in **Figure 7.14b** (Fyhn et al., 2008; Hafting et al., 2005).

One possible function of grid cells is to provide information about the direction of movement (Moser, Moser, et al., 2014;



(a) Explore maze (b) Turn right for food (c) Turn left for food

Figure 7.13 Maze used by Tolman. (a) The rat initially explores the maze. (b) The rat learns to turn right to obtain the food at B when it starts at A. (c) When placed at C, the rat turns left to reach the food at B. In this experiment, precautions were taken to prevent the rat from knowing where the food was based on cues such as smell.

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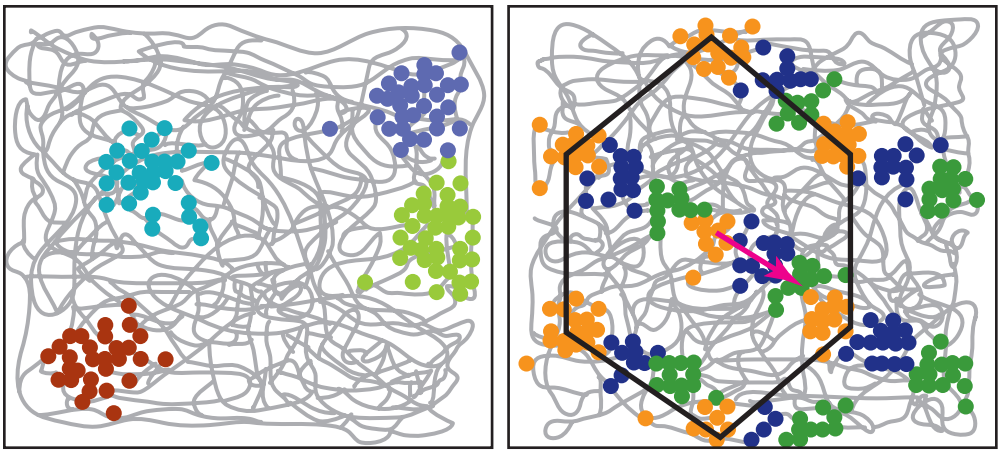

(a) (b)

Figure 7.14 A record similar to those O'Keefe produced by recording from neurons in a rat's hippocampus as it walked inside a box. (a) The path taken by a rat in a box is outlined in gray. The positions within the box where four place cells fired are highlighted by red, blue, purple, and green dots. (b) The positions within the box where three grid cells fired are denoted by orange, blue, and green dots. See text for details.

Moser, Roudi, et al., 2014). For example, movement along the pink arrow would lead to responses in the "orange cell," then the "blue cell," and then the "green cell." Movement in other directions would result in different patterns of firing across grid cells. Thus, grid cells may be able to code distance and direction information as an animal moves, and place cells and grid cells probably work together, because they are connected with each other.

There is much left to learn about these cells and their interconnections, but these discoveries are already recognized as being so important that John O'Keefe, May-Britt Moser, and Edvard Moser were jointly awarded the 2014 Nobel Prize in Physiology or Medicine for their discovery of place and grid cells.

What makes these place and grid cells especially important is that recent experiments suggest that similar cells may also exist in humans. Joshua Jacobs and coworkers (2013) found neurons in humans similar to the rat grid cells by recording from single neurons in patients, like those described in Chapter 4 (p. 85), who were being prepared for surgery to treat severe epilepsy. **Figure 7.15** shows the results for a neuron in one patient's entorhinal cortex. The red areas, which indicate high firing frequency, form a grid pattern similar to what occurs in the rat. Although the human patterns are "noisier" than the rats', the results from 10 different patients led Jacobs to conclude that these neurons, like the rat grid cells, help humans create maps of the environment. Cells similar to rat place cells have also been discovered in humans (Ekstrom et al., 2003). So the next time you have to navigate along a route, give credit both to your knowledge of landmarks and to neurons that are signaling where you are and where you are going.

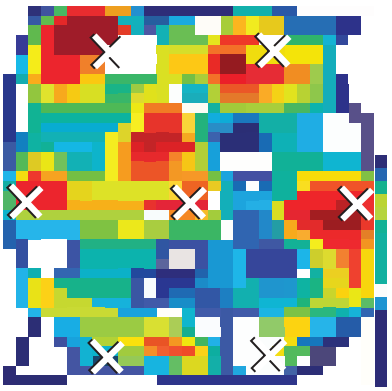

Figure 7.15 Colors indicate firing of a neuron in a participant's entorhinal cortex at locations in the area that the participant was visiting in the virtual environment. Red indicates the locations associated with a high firing rate. Note that they are arranged in a hexagonal layout, similar to what was observed in earlier experiments on rats. (From Jacobs et al., 2013)

Individual Differences in Wayfinding

Just as different people have different mental abilities, wayfinding ability varies from one individual to another. One difference in wayfinding can be traced to experience. People who have practiced getting from one place to another in a particular environment are often good at finding their way. This effect of practice was linked to physiology in an experiment by Eleanor Maguire and coworkers (2006) who studied two groups of participants: (1) London bus drivers, who have learned specific routes through the city, and (2) London taxi drivers, who have to travel to many different places throughout the city. **Figure 7.16a** shows the results of an experiment in which bus drivers and taxi drivers were asked to identify pictures of London landmarks. Taxi drivers scored higher than bus drivers, as we might expect from their more widespread exposure to London. And when the bus and taxi drivers' brains were then scanned, Maguire found that the taxi drivers had greater volume in the back of their hippocampus (posterior) (**Figure 7.16b**) and less volume in the front (anterior).

This result is similar to the results of the experience-dependent plasticity experiments described in Chapter 4. Remember that kittens reared in an environment of vertical stripes had more neurons in their cortex that responded to vertical stripes (see Figure 4.11, page 74). Similarly, taxi drivers who have extensive experience navigating have a larger

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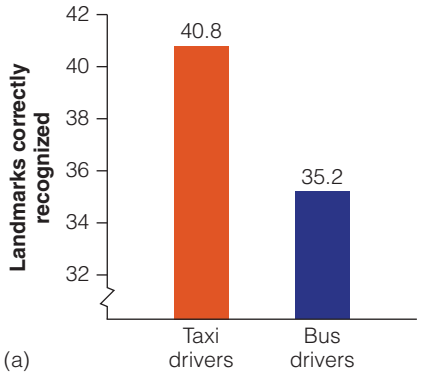

Figure 7.16 (a) Performance on a landmark test by London taxi drivers and bus drivers. A perfect score is 48. (b) Cross section of the brain. Yellow indicates greater hippocampus volume in London taxi drivers compared to London bus drivers, as determined by magnetic resonance imaging. (From Maguire et al., 2006)

posterior hippocampus. Importantly, drivers with the largest posterior hippocampus were the ones with the most years of experience. This final result provides strong support for experience-dependent plasticity (more experience creates a larger hippocampus) and rules out the possibility that it is simply that people with a larger hippocampus are more likely to become taxi drivers than bus drivers.

Is there any evidence for hippocampus-related navigation differences among non-taxi-drivers? Iva Brunec and coworkers (2019) answered this question by giving a questionnaire to a group of young adults to measure their reliance on map-based strategies when navigating. For example, they were asked, "When planning a route, do you picture a map of your route?" People who scored higher on using mapping strategies performed better on a navigation test, and also had larger posterior hippocampus and smaller anterior, just like the London taxi drivers.

When taken together, the important message of all of these studies is that wayfinding is multifaceted. It depends on numerous sources of information and is distributed throughout many structures in the brain. This isn't surprising when we consider that wayfinding involves seeing and recognizing objects along a route (perception), paying attention to specific objects (attention), using information stored from past trips through the environment (memory), and combining all this information to create maps that help us relate what we are perceiving to where we are now and where we are planning to go next.

TEST YOURSELF 7.1

1. What is the moral of the story about sea squirts?
2. What was J. J. Gibson's motivation for establishing the ecological approach to perception?
3. What is optic flow? What are two characteristics of optic flow? Describe the experiment that considered whether people can use optic flow to determine their heading.
4. What is invariant information? How is invariance related to optic flow?
5. What is observer-produced information? Describe its role in somersaulting and why there is a difference between novices and experts when they close their eyes.
6. What is the point of the "keeping your balance" demonstration?
7. Describe the swinging room experiments. What principles do they illustrate?
8. What is an affordance? Describe the results of the experiments on patient M.P. that illustrate the possible operation of affordances.
9. Describe the experiment that compared the EEG response to manipulable tools and other objects. What is an action affordance?
10. What does research on walking and driving a car tell us about how optic flow may (or may not) be used in navigation? What are some other sources of information for navigation?
11. What is wayfinding? Describe Hamid's research on looking at landmarks.
12. Describe Janzen and van Turennout's experiment in which they measured people's brain activity when remembering objects they had seen while navigating through a computer simulated museum. What did Janzen and van Turennout conclude about the brain and navigation?
13. What did Tolman's rat maze experiment demonstrate?
14. Describe the rat experiments that discovered place cells and grid cells. How might these cells help rats navigate?
15. Describe Jacobs and coworkers' experiment that provided evidence for human grid cells.
16. Describe the taxi-driver experiment and the experiment on non-taxi drivers. What did each experiment reveal about the physiology of individual differences in wayfinding?
17. What does it mean to say that wayfinding is "multifaceted"? How does wayfinding reveal interactions between perception, attention, memory, and action?

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7.4 Interacting With Objects: Reaching, Grasping, and Lifting

So far, we have been describing how we move around in the environment—driving a car, walking, navigating from one place to another. But another aspect of action is interacting with objects in the environment. To discuss how people interact with objects, we will consider the sequence of events in **Figure 7.17**, in which the following events occur, culminating in an extremely important behavior—depositing a dollop of ketchup on a burger!

(a) Reaching toward the bottle
(b) Grasping the bottle
(c) Lifting and tilting the bottle
(d) Using the other hand to hit the bottle to deposit the ketchup on the burger

We usually accomplish the sequence in Figure 7.17 rapidly and without thinking. But as we will see, getting the ketchup onto the burger involves multiple senses, commands sent from the motor area of the brain to create movement, and predictive mechanisms that involve corollary discharge signals like the ones we described in Chapter 6 (p. 128), which help create accurate reaching and lifting and which help adjust the grip so the ketchup bottle is gripped firmly. We begin with reaching and grasping.

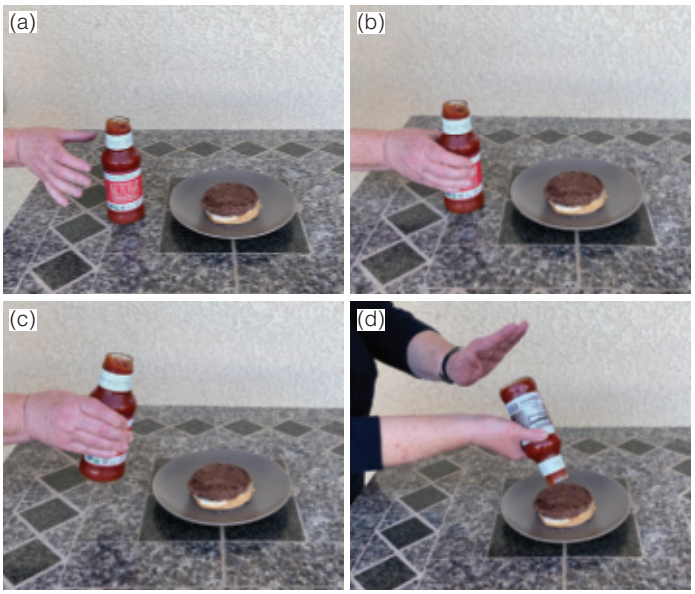

Figure 7.17 Steps leading to depositing a dollop of ketchup on a hamburger. The person (a) reaches for the bottle with her right hand, (b) grasps the bottle, (c) lifts the bottle, and (d) delivers a "hit" to the bottle that has been rotated so it is over the hamburger.

Reaching and Grasping

Reaching for the bottle is the first step. One way to understand reaching and grasping is to look at what's going on in the brain.

Brain Areas for Reaching and Grasping An important breakthrough in studying the physiology of reaching and grasping came with the discovery of the ventral (*what*) and dorsal (*where/how/action*) pathways described in Chapter 4 (see Figure 4.23, page 80). Remember that D.F., who had damage to her ventral pathway, had difficulty recognizing objects or judging their orientation, but she could "mail" an object by placing it through an oriented opening. The idea that there is one processing stream for perceiving objects and another for acting on them helps us understand what is happening when a person reaches for the ketchup bottle.

The first step, identifying the bottle among the other things on the table, involves the ventral (what) pathway. The next step, reaching for the bottle, involves the dorsal (action) pathway. As reaching progresses, the location of the bottle and its shape are perceived using the ventral pathway and positioning the fingers to grasp the bottle involves the dorsal pathway. Thus, reaching for and grasping the bottle involves continuously perceiving the shape and position of the bottle, shaping the hand and fingers relative to the bottle, and calibrating actions in order to grasp the bottle (Goodale, 2011).

But this interaction between the dorsal and ventral pathways isn't the whole story. Specific areas of the brain are involved in reaching and grasping. One of the most important areas of the brain for reaching and grasping is the parietal lobe. The area in the monkey parietal lobe involved in reaching is called the parietal reach region (PRR) (**Figure 7.18**).

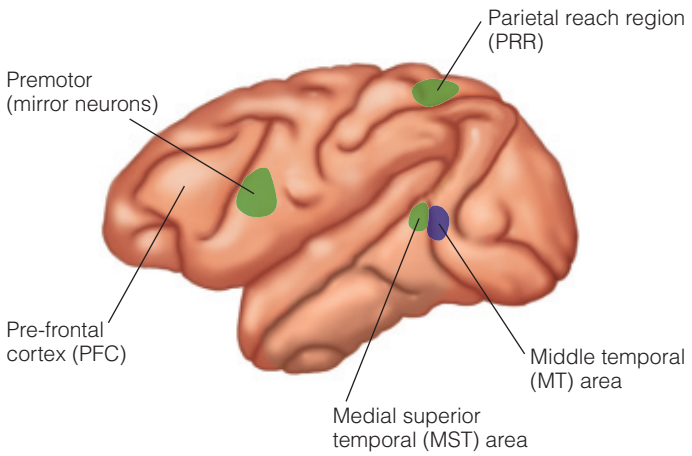

Figure 7.18 Monkey cortex showing location of the parietal reach region (PRR) and the area of premotor cortex where mirror neurons were found. In addition, two areas involved in motion perception, the middle temporal (MT) area and the medial superior temporal (MST) area, are shown. These areas will be discussed in Chapter 8.

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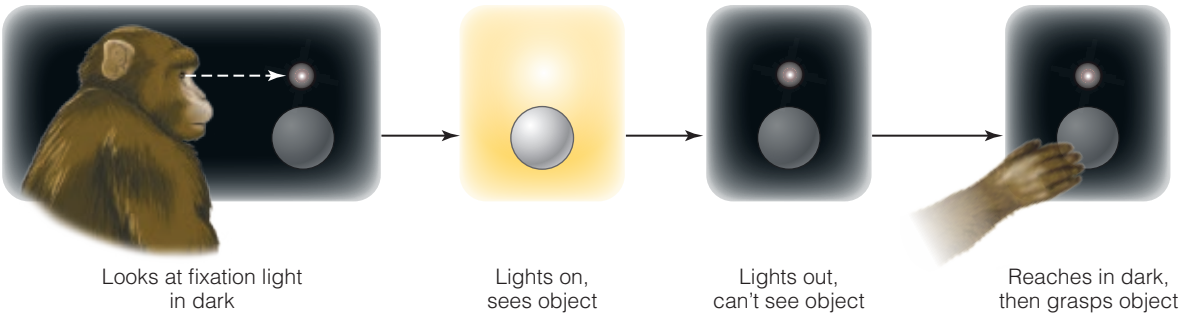

Figure 7.19 The monkey's task in Fattori and coworkers' (2010) experiment. The monkey always looked at the small light above the sphere. The monkey sees the object to be grasped when the lights go on, then reaches for and grasps the object once the lights go off and the fixation light changes color. (From Fattori et al., 2010)

This region contains neurons that control not only reaching but also grasping (Connelly et al., 2003; Vingerhoets, 2014). Evidence suggests that there are a number of regions like the monkey's parietal reach regions in the human parietal lobe (Filimon et al., 2009).

Recording from single neurons in a monkey's parietal lobe has revealed neurons in an area next to the parietal reach region that respond to specific types of hand grips. This was determined by Patricia Fattori and coworkers (2010) using the procedure shown in **Figure 7.19**: (1) The monkey observed a small fixation light in the dark; (2) lights were turned on for half a second to reveal the object to be grasped; (3) the lights went out and then, (4) after a brief pause, the fixation light changed color, signaling that the monkey should reach for the object.

The key part of this sequence occurred when the monkey reached for the object in the dark. The monkey knew what the object was from seeing it when the lights were on (a round ball in this example), and so while reaching for it in the dark, shaped its grip to match the object. A number of different objects were used, as shown in **Figure 7.20a**, each of which required a different grip.

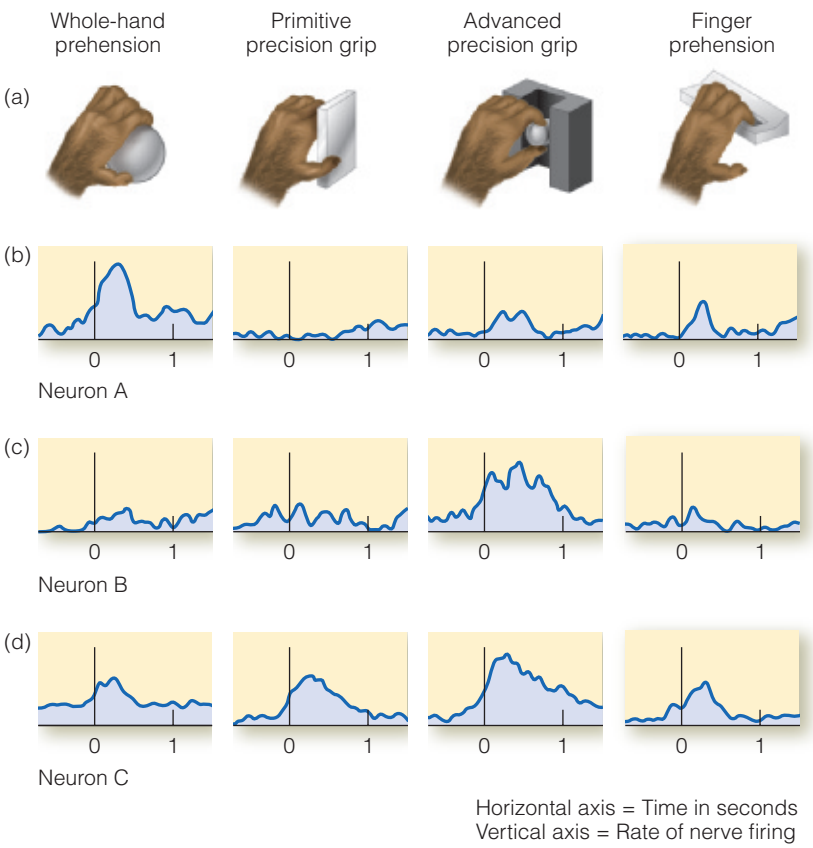

Figure 7.20 Results of Fattori and coworkers' (2010) experiment showing how three different neurons respond to reaching and grasping of four different objects. (a) Four objects. The type of grasping movement associated with each object is indicated above the object. (b) Response of neuron A to grasping each object. This neuron responds best to whole-hand prehension. (c) Response of neuron B, which responds best to advanced precision grip. (d) Response of neuron C, which responds to all four types of grasping.

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The key result of the experiment is that there are neurons that respond best to specific grips. For example, neuron A (**Figure 7.20b**) responds best to "whole-hand prehension," whereas neuron B (**Figure 7.20c**) responds best to "advanced precision grip." There are also neurons, like C (**Figure 7.20d**), that respond to a number of different grips. Remember that these neurons were firing as the monkey was reaching for the object in the dark, so the firing was caused not by visual stimulation, but by the monkey's prediction of what the object's shape would be when it was grasped.

In a follow-up experiment on the same monkeys, Fattori and coworkers (2012) discovered neurons that responded not only when a monkey was preparing to grasp a specific object, but also when the monkey *viewed* that specific object. An example of this type of neuron, which Fattori calls visuomotor grip cells, is a neuron that initially responds when the monkey sees a specific object and then also responds as the monkey is forming its hand to grasp the same object. This type of neuron is therefore involved in both perception (identifying the object and/or its affordances by seeing) and action (reaching for the object and gripping it with the hand) (also see Breveglieri et al., 2018).

Proprioception We've seen that there are brain areas and neurons that are involved in guiding the hand on its way to grasp an object. But there's also another mechanism that helps keep the hand on course. That mechanism is proprioception—the ability to sense body position and movement. Proprioception depends on neurons located throughout the body, such as the ones shown in **Figure 7.21** for the human limb. Proprioceptive receptors in the elbow joint, muscle spindle, and tendon sense the position and movement of the arm.

We take proprioception for granted, because it operates without our conscious involvement, but when the sense of proprioception is lost the results are disastrous, as illustrated by the case of Ian Waterman, who at the age of 19, suffered complications accompanying the flu that damaged sensory neurons from his neck down. Ian was unable to sense the position of his limbs and also lost the sense of touch on his body. Thus, although Ian could still contract his muscles, he was unable to coordinate his movements. After years of training he was eventually able to carry out actions, but to do this he had to depend solely on his sense of vision to monitor the position and movement of his limbs.

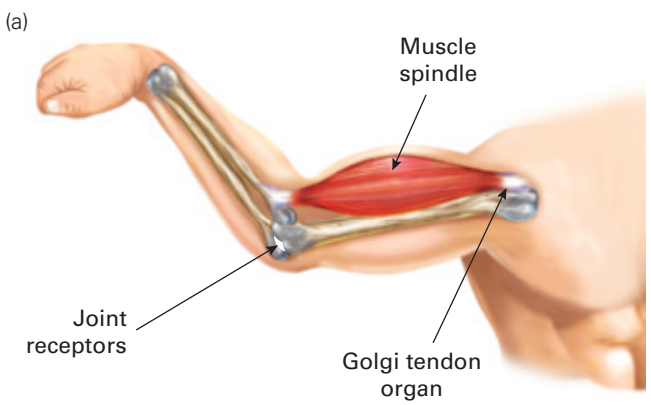

Figure 7.21 Proprioceptive neurons are located in the elbow joint, tendon, and muscle spindle of the arm. (Based on Tuthill & Azim, 2018)

Ian's need to constantly visually monitor his movements is quite different than what happens if proprioception is available, because as you reach for something, you have two sources of information in addition to visual information: (1) proprioceptive information, which also provides information about the position of your hand and arm, and (2) corollary discharge (CD) signals. Remember from Chapter 6 that when signals are sent from the motor area to move the eye muscles, a CD signal provides advance information about how the eyes are going to move. For reaching and grasping, when signals are sent from the motor area to move the arm and hand, a CD signal provides advance information about the movement that helps keep the arm and hand movements on course toward their goal (Tuthill & Azim, 2018; Wolpert & Flanagan, 2001).

Figure 7.22 shows what happens to reaching if the CD isn't available. In this experiment, the participant reaches to the right until they hear a tone, which signals that they should reach to the left for the target. Participants could do this accurately, as indicated by the blue line. But if the CD signals are disrupted by electrical stimulation of the cerebellum, a structure important for controlling motor functioning, the reach misses the target, as indicated by the red line (Miall et al., 2007; Shadmehr et al., 2010). **Table 7.1** summarizes the three sources of information that help guide our hand toward a target.

Lifting the Bottle

Once the bottle in Figure 7.17 is grasped, it is lifted, and the person makes a prediction to determine the force of the lift. This prediction takes into account the size of the bottle, how full it is, and past lifting experiences with similar objects. Thus, different predictions occur if the bottle is full or almost empty, and if the prediction is accurate, the bottle will be lifted with just the right force. However, what if the person thinks the bottle is full, but it turns out to be almost empty? In this situation the person uses too much force, so the lift is too high.

Table 7.1 Signals That Help Guide Reaching

SIGNAL	PURPOSE
Visual	Monitor hand position
Proprioceptive	Sense hand/arm position
Corollary discharge	Provide information from motor signals about where hand/arm is going to move

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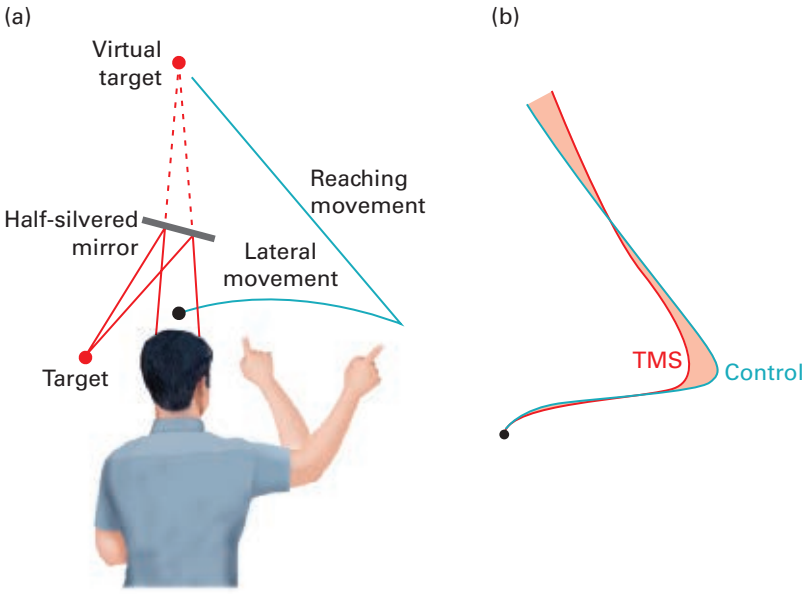

Figure 7.22 (a) The participant moves the arm to the right and then, responding to a tone, reaches for the target. (b) Blue line = accurate reaching. Red line = how reach is thrown off course when CD signal is disrupted by electrical stimulation. (From Shadmehr, et al., 2010)

This effect of erroneously predicting weight is demonstrated by the **size-weight illusion**, in which a person is presented with two weights. The weight on the left is small and the weight on the right is large, but their weights are exactly the same (**Figure 7.23**). The person is told to grasp the handles on top of each weight and, when he hears a signal, to lift them simultaneously. What happens next surprises him, because he lifts the large weight on the right much higher than the small weight on the left and says that the larger weight feels lighter. (Remember that both weights are actually the same weight.) Thus, the size-weight illusion, which was first described by French physician Augustin Charpentier in 1891, shows that when observing two differently sized objects, we predict that the larger one will be heavier, so we exert more force to lift it, causing it to be lifted higher and, surprisingly, to feel lighter (Buckingham, 2014).

Adjusting the Grip

Once the bottle has been lifted and rotated, so it is poised above the burger, we are ready to dispense the ketchup. The ketchup, however, is not cooperating, so a swift hit delivered by the other hand (**Figure 7.24**) is needed to get it to leave the bottle. It is important, of course, to grip the bottle firmly

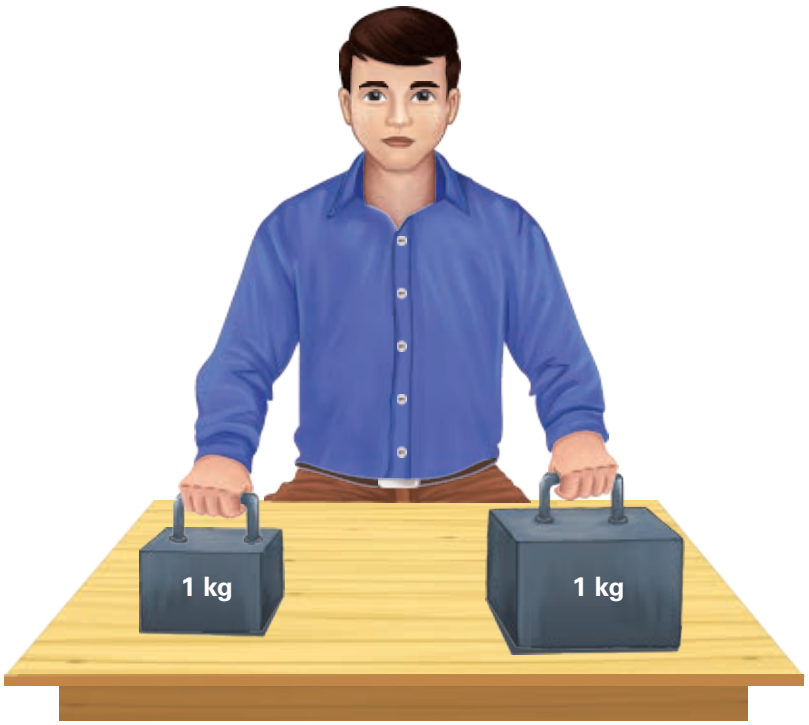

Figure 7.23 This person, who is getting ready to simultaneously lift the two weights, is about to experience the size-weight illusion, because both weights are the same weight, even though they differ in size.

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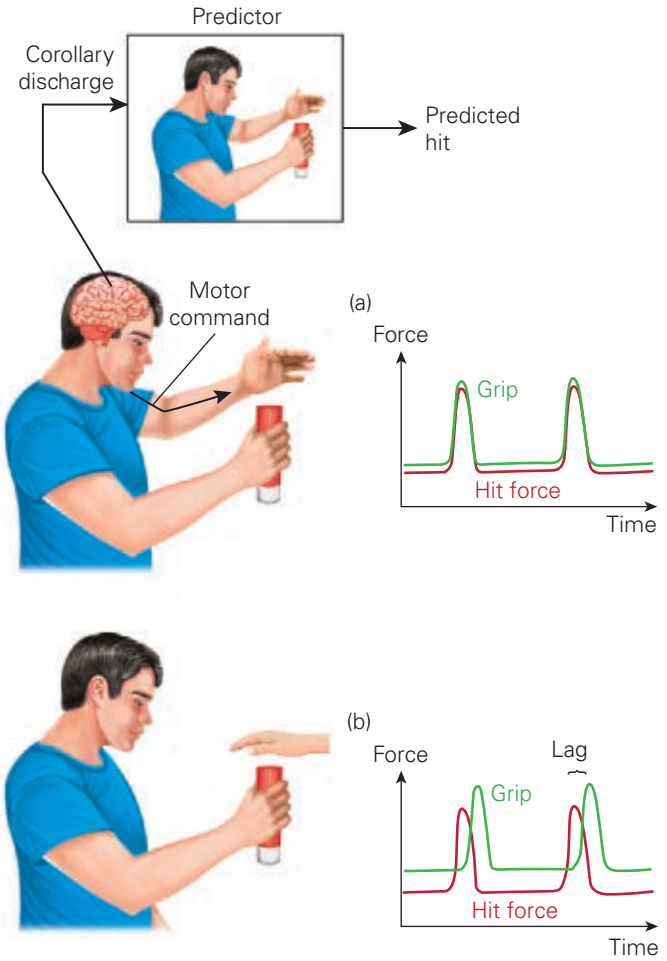

Figure 7.24 (a) A person getting ready to hit the bottom of the ketchup bottle. The motor command being sent to the hitting (left) hand is accompanied by a corollary discharge which predicts the force of the upcoming hit. This prediction causes the motor command sent to the right hand (not shown) to grip the bottle with a force (green) that closely matches the force and timing of the hit (red), so the bottle is held tight when the hit is delivered. (b) When someone else hits the bottle, there is no prediction of the force of the upcoming hit, so the grip force lags behind the hit force and must be increased to prevent slippage. (From Wolpert & Flanagan, 2001)

so the hit won't cause the bottle to slip. **Figure 7.24a** shows that when the person delivers the hit, the force of the grip (green) increases exactly when the hit is delivered (red). However, **Figure 7.24b** shows that when someone else delivers the hit, the increase in grip lags behind the hit. Why is the grip adjusted quickly and accurately in (a)? Because a corollary discharge provides information about the timing and force of the hit. When someone else delivers the hit, there is no CD, so there is no prediction of what is going to happen.

Simple actions that we carry out every day therefore depend on constant interactions between sensory and motor components of the nervous system, and constant prediction of what's going to happen next: how far to reach, how to adjust your hand to grasp things properly, how hard to grip, all of which depend on the objects involved and the upcoming task. Thus, picking up a pen to write involves a different configuration of the fingers and force of grip than picking up the ketchup bottle or picking up a pen to move it to another place on your desk. Considering the number of actions you carry out every day, there is a lot of prediction going on. Luckily you usually don't have to think about it because your brain takes care of it for you.

7.5 Observing Other People's Actions

We not only take action ourselves, but we regularly watch other people take action. This "watching others act" is most obvious when we watch other people's actions on TV or in a movie, but it also occurs any time we are around someone else who is doing something. One of the most exciting outcomes of research studying the link between perception and action was the discovery of neurons in the premotor cortex (Figure 7.18) called *mirror neurons*.

Mirroring Others' Actions in the Brain

In the early 1990s, a research team led by Giacomo Rizzolatti was investigating how neurons in the monkey's premotor cortex fired as the monkey performed actions like picking up a toy or a piece of food. Their goal was to determine how neurons fired as the monkey carried out specific actions. But as sometimes happens in science, they observed something they didn't expect. When one of the experimenters picked up a piece of food while the monkey was watching, neurons in the monkey's cortex fired. What was so unexpected was that the neurons that fired to observing the experimenter pick up the food were the same ones that had fired earlier when the monkey had itself picked up the food (Gallese et al., 1996).

This initial observation, followed by many additional experiments, led to the discovery of **mirror neurons**—neurons that respond both when a monkey observes someone else grasping an object such as food on a tray (**Figure 7.25a**) and when the monkey itself grasps the food (**Figure 7.25b**; Rizzolatti et al., 2006). They are called mirror neurons because the neurons' response to watching the experimenter grasp an object is similar to the response that would occur if the monkey were performing the same action. Just looking at the food causes no response, and watching the experimenter grasp the food with a pair of pliers, as in **Figure 7.25c**, causes only a small response (Gallese et al., 1996; Rizzolatti et al., 2000). This last result indicates that mirror neurons can be specialized to respond to only one type of action, such as grasping or placing an object somewhere.

Simply finding a neuron that responds when an animal observes a particular action doesn't tell us why the neuron is firing, however. For example, we could ask if the mirror neurons in Rizzolatti's study were responding to the anticipation of receiving food rather than to the experimenter's specific actions. It turns out that this cannot be a reasonable explanation

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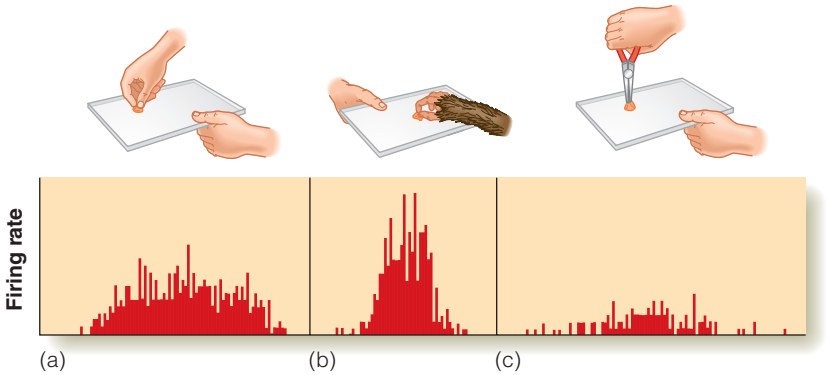

Figure 7.25 Response of a mirror neuron. (a) Response to watching the experimenter grasp food on the tray. (b) Response when the monkey grasps the food. (c) Response to watching the experimenter pick up food with a pair of pliers. (From Rizzolatti et al., 2000)

because the type of object made little difference. The neurons responded just as well when the monkey observed the experimenter pick up an object that was not food.

But could the mirror neurons simply be responding to the pattern of motion? The fact that the neuron does not respond when watching the experimenter pick up the food with pliers argues against this idea. Further evidence that mirror neurons are doing more than just responding to a particular pattern of motion is the discovery of neurons that respond to sounds that are *associated with* actions. These neurons in the premotor cortex, called **audiovisual mirror neurons**, respond when a monkey performs a hand action *and* when it hears the sound associated with this action (Kohler et al., 2002). For example, the results in **Figure 7.26** show the response of a neuron that fires (a) when the monkey sees and hears the experimenter break a peanut, (b) when the monkey just sees the experimenter break the peanut, (c) when the monkey just hears the sound of the breaking peanut, and (d) when the *monkey* breaks the peanut. What this means is that just *hearing* a peanut breaking or just *seeing* a peanut being broken causes activity that is also associated with the perceiver's *action* of breaking a peanut. These neurons are responding, therefore, to what is "happening"—breaking a peanut—rather than to a specific pattern of movement.

At this point you might be asking whether mirror neurons are also present in the human brain. After all, we've only been talking about monkey brains so far. Some research with humans does suggest that our brains also contain mirror neurons. For example, researchers using electrodes to record the brain activity in people with epilepsy in order to determine which part of their brains was generating their seizures have recorded activity from neurons with the same mirror properties as those identified in monkeys (Mukamel et al., 2010). Additional work using fMRI in neurologically normal individuals has further suggested that these neurons are distributed throughout the frontal, parietal, and temporal lobes (**Figure 7.27**) in a network that has been broadly called the **mirror neuron system** (Caspers et al., 2010; Cattaneo & Rizzolatti, 2009; Grosbras et al., 2012; Molenberghs et al., 2012). However, a great deal more research is needed to determine if and how this mirror neuron system supports perception and action in humans. In the next section, we highlight some of the work that seems promising in identifying the role mirror neurons play in human perception and performance.

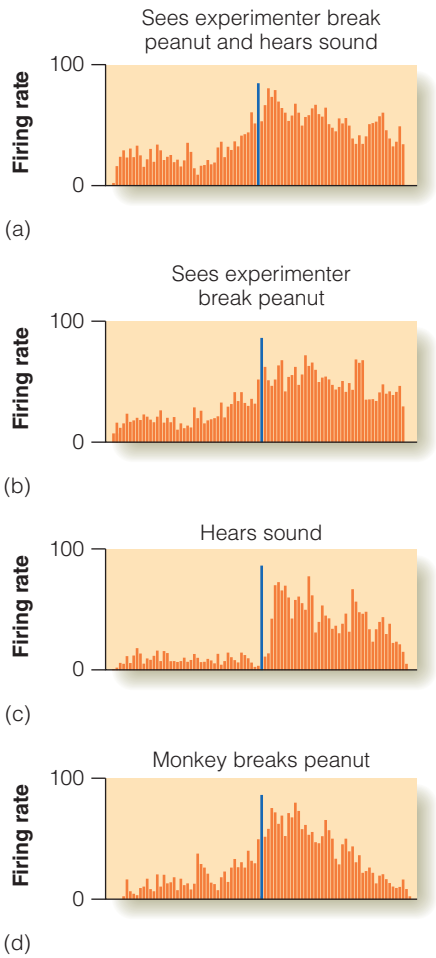

Figure 7.26 Response of an audiovisual mirror neuron to four different stimuli. (From Kohler et al., 2002)

Predicting People's Intentions

Some researchers have proposed that there are mirror neurons that respond not just to *what* is happening but to *why* something is happening, or more specifically, to the *intention* behind what is happening. To understand what this means, let's visit a coffee shop and observe a person reaching for her coffee cup. Why, we might wonder, is she reaching for the cup? One obvious answer is that she intends to drink some coffee, although

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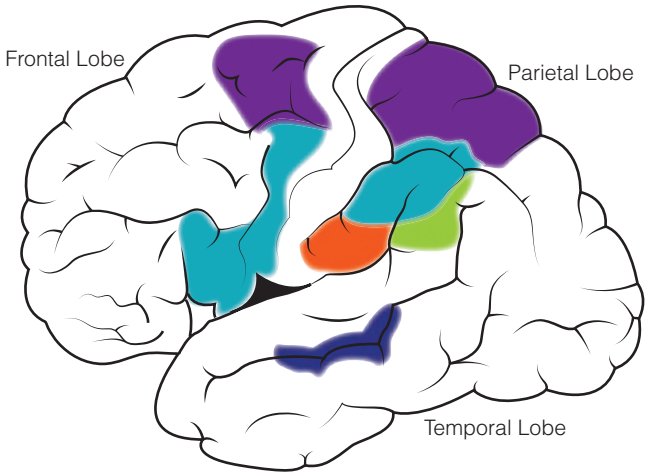

Figure 7.27 Cortical areas in the human brain associated with the mirror neuron system. Colors indicate the type of actions processed in each region: From top down: Purple, reaching; Blue, upper limb movements; Orange, tool use; Green, movements not directed toward objects; Dark blue, upper limb movements. (Adapted from Cattaneo & Rizzolatti, 2009)

if we notice that the cup is empty, we might instead decide that she is going to take the cup back to the counter to get a refill, or if we know that she never drinks more than one cup, we might decide that she is going to place the cup in the used cup bin. Thus, there are a number of different intentions that may be associated with the same action.

What is the evidence that the response of mirror neurons can be influenced by different intentions? Mario Iacoboni and coworkers (2005) did an experiment in which they measured participants' brain activity as they watched short film clips represented by the stills in **Figure 7.28**. Stills for the two Intention films, on the right, show a hand reaching in to pick up a cup. But there is an important difference between the two scenes. In the top panel, the table is neatly set up, the food is untouched, and the cup is full of tea. In the bottom panel, the table is a mess, the food has been eaten, and the cup appears to be empty. Iacoboni hypothesized that viewing the top film would lead the viewer to infer that the person was picking up the cup to drink from it and viewing the bottom film would lead the viewer to infer that the person was picking up the cup to clean up.

Iacoboni's participants also viewed the control films shown in the other panels. The Context control film showed the table setting, and the Action control film showed the hand reaching in to pick up an isolated cup. The reason these two types of films were presented was that they contained the visual elements of the intention films, but didn't suggest a particular intention.

Figure 7.29 shows the brain response for the intention films and the control films. The key result is that there was a significant difference between the response to the drinking and cleaning up films, but there was no difference between the before tea and after tea context films. Based on the difference in activity between the two Intention conditions, Iacoboni concluded that the mirror neuron area is involved with understanding the intentions behind the actions shown in the films. He reasoned that if the mirror neurons were just signaling the action of picking up the cup, then a similar response would occur regardless of whether a context surrounding the cup was present. Mirror neurons, according to Iacoboni, code the "why" of actions and respond differently to different intentions.

If mirror neurons do, in fact, signal intentions, how do they do it? One possibility is that the response of these neurons is determined by the chain of motor activities that could be *expected* to happen in a particular context (Fogassi et al., 2005; Gallese, 2007). For example, when a person picks up a cup with the intention of drinking, the next expected actions would be to bring the cup to the mouth and then to drink some coffee or tea. However, if the intention is to clean up, the expected action might be to carry the cup over to the sink. According to this

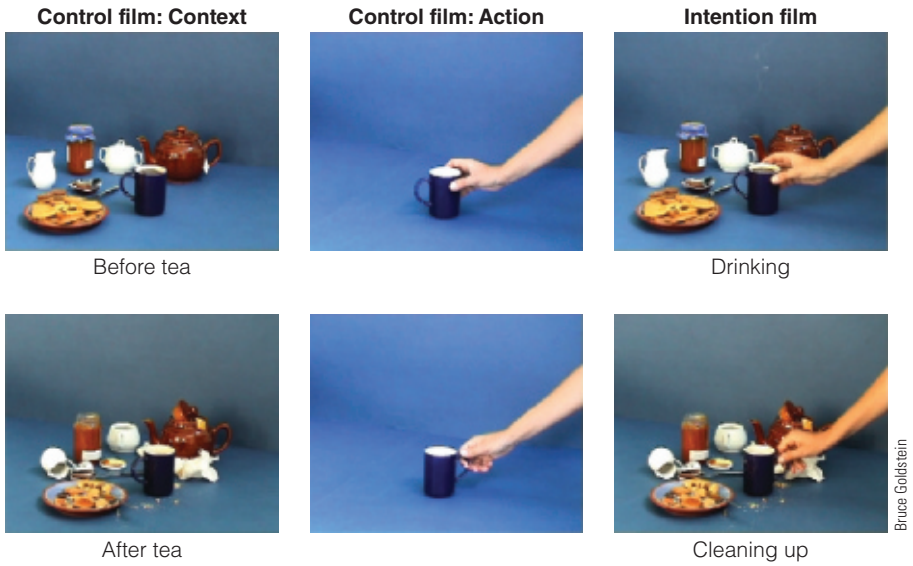

Figure 7.28 Images from the Context, Action, and Intention film clips viewed by Iacoboni and coworkers' (2005) participants. Each column corresponds to one of the experimental conditions. In the Context condition there were two clips, before tea (everything in its place) and after tea (a mess). In the Action condition the two types of grips (whole hand and using the handle) were shown an equal number of times. In the Intention condition, the "drinking" context was the same as "before tea" but with the hand added. The "cleaning up" context corresponded to "after tea." The two types of hand grips (whole hand and using the handle) were shown an equal number of times during the "drinking" and "cleaning" clips. (From Iacoboni et al., 2005)

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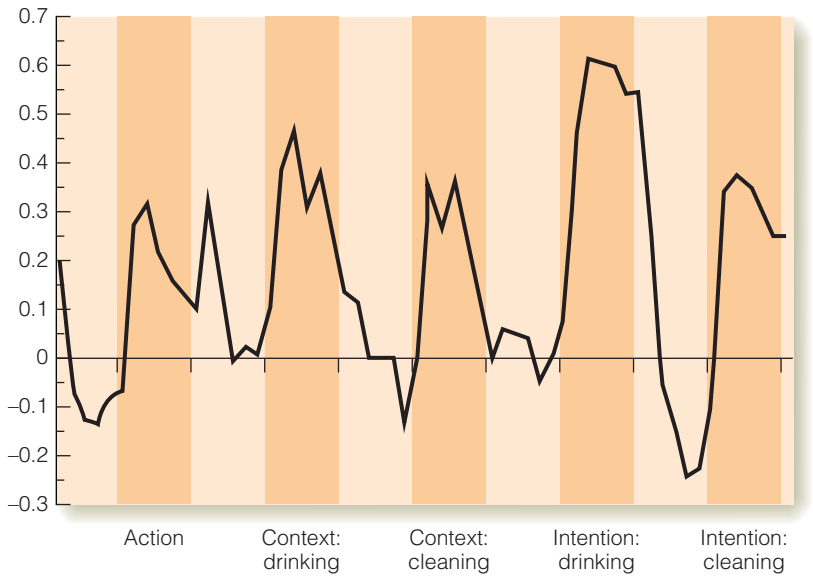

Figure 7.29 Iacoboni and coworkers' (2005) results, showing the brain response for the Action, Drinking, and Cleaning conditions. The important result is that for the intention condition, the drinking response is significantly larger than the cleaning response. However, there is no difference between drinking and cleaning for the context condition.

idea, mirror neurons that respond to different intentions are responding to the action that is happening *plus* the sequence of actions that is most likely to follow, given the context.

The exact functions of mirror neurons in humans are still being actively researched (Caggiano et al., 2009; Rizzolati & Singaglia, 2016). In addition to proposing that mirror neurons signal what is happening as well as the intentions behind various actions, researchers have also proposed that mirror neurons help us understand (1) communications based on facial expressions (Buccino et al., 2004; Ferrari et al., 2003); (2) emotional expressions (Dapretto et al., 2006); (3) gestures, body movements, and mood (Gallese, 2007; Geiger et al., 2019); (4) the meanings of sentences (Gallese, 2007); and (5) differences between ourselves and others (Uddin et al., 2007). As might be expected from this list, it has also been proposed that mirror neurons also play an important role in guiding social interactions (Rizzolatti & Sinigaglia, 2010; Yoshida et al., 2011) and that disorders characterized by impaired social interactions such as autism spectrum disorder may be associated with abnormal functioning of the mirror neuron system (Oberman et al., 2005, 2008; Williams et al., 2001).

As with any newly discovered phenomenon, the function of mirror neurons is a topic of debate among researchers. Some researchers propose that mirror neurons play important roles in human behavior (as noted above), and others take a more cautious view (Cook et al., 2014; Hickock, 2009). One of the criticisms of the idea that mirror neurons determine people's intentions is that the mirror neuron response occurs so rapidly after observing an action that there's not enough time to understand the action. It has, therefore, been suggested that mirror neurons could help detect and recognize an action but that then a slower process may be needed to achieve an understanding of a person's intentions behind the action (Lemon, 2015).

Consider that when feature detectors that respond to oriented moving lines were discovered in the 1960s, some researchers proposed that these feature detectors could explain how we perceive objects. With the information available at the time, this was a reasonable proposal. However, later, when neurons that respond to faces, places, and bodies were discovered, researchers revised their initial proposals to take these new findings into account. In all likelihood, a similar process will occur for mirror neurons. Some of the proposed functions will be confirmed, but others may need to be revised.

7.6 Action-Based Accounts of Perception

The traditional approach to perception has focused on how the environment is *represented* in the nervous system and in the perceiver's mind. According to this idea, the purpose of visual perception is to create a representation in the mind of whatever we are looking at. Thus, if you look at a scene and see buildings, trees, grass, and some people, your perception of the buildings, trees, grass, and people is representing what is "out there," and so accomplishes vision's purpose of representing the environment.

But as you might have suspected after reading this chapter, many researchers believe that the purpose of vision is not to create a representation of what is out there but to guide our actions that are crucial for survival (Brockmole et al., 2013; Goodale, 2014; Witt, 2011a).

The idea that action is crucial for survival has been described by Melvyn Goodale (2011) as follows: "Many researchers now understand that brains evolved not to enable us to think, but to enable us to move and interact with the world. Ultimately, all thinking (and by extension, all perception) is in the service of action" (p. 1583). According to this idea, perception may provide valuable information about the environment, but taking a step beyond perception and acting on this

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information enables us to survive so we can perceive another day (Milner & Goodale, 2006).

The idea that the purpose of perception is to enable us to interact with the environment has been taken a step further by researchers who have turned the equation around from "action depends on perception" to "perception depends on action." The **action-specific perception hypothesis** (Witt, 2011a) states that people perceive their environment in terms of their ability to act on it. This hypothesis has been largely based on the results of experiments involving sports. For example, Jessica Witt and Dennis Proffitt (2005) presented a series of circles to softball players just after they had finished a game, and asked them to pick the circle that best corresponded to the size of a softball. When they compared the players' estimates to their batting averages from the just-completed game, they found that batters who hit well perceived the ball to be bigger than batters who were less successful.

Other experiments have shown that tennis players who have recently won report that the net is lower (Witt & Sugovic, 2010) and participants who were most successful at kicking football field goals estimated the goal posts to be farther apart (Witt & Dorsch, 2009). The field goal experiment is especially interesting because the effect occurred only after they had attempted 10 field goals. Before they began, the estimates of the poor kickers and the good kickers were the same.

These sports examples all involved making judgments after doing either well or poorly. This supports the idea that perception can be affected by performance. What about situations in which the person hasn't carried out any action but has an expectation about how difficult it would be to perform that action? For example, what if people who were physically fit and people who were not physically fit were asked to estimate distances? To answer this question, Jessica Witt and coworkers (2009) asked people with chronic back and/or leg pain to estimate their distance from various objects placed in a long hallway. Compared to people without pain, the chronic pain group consistently overestimated their distance from objects. The reason for this, according to Witt, is that over time people's general fitness level affects their perception of how difficult it will be to carry out various sorts of physical activity, and this in turn affects their perception of the activity. Thus, people with pain that makes walking difficult will perceive an object as being farther away, even if they are just looking at the object. Also, older people, who generally have less physical ability than younger people, estimate distances to be farther compared to younger adults (Sugovic & Witt, 2013).

Some researchers, however, question whether the perceptual judgments measured in some of the experiments we have described are actually measuring perception. Participants in these experiments might, they suggest, be affected by "judgment bias," caused by their expectations about what they think would happen in a particular situation. For example, participants' *expectation* that objects could appear farther when a person has difficulty walking might cause them to *say* the object appears farther, even though their *perception* of distance was actually not affected (Durgin et al., 2009, 2012; Loomis & Philbeck, 2008; Woods et al., 2009).

This explanation highlights a basic problem in measuring perception in general: Our measurement of perception is based on people's responses, and there is no guarantee that these responses accurately reflect what a person is perceiving. Thus, as pointed out above, there may be some instances in which participants' responses reflect not what they are perceiving, but what they think they should be perceiving. For this reason, researchers have tried very hard to conduct experiments in which the effects of action have been demonstrated even when there are no obvious expectations or task demands (Witt, 2011a, 2011b; Witt et al., 2010). A reasonable conclusion, taking a large number of experiments into account, is that in some experiments participants' judgments may be affected by their expectations, but in other experiments their judgments may reflect a real relationship between their ability to act and their perception.

SOMETHING TO CONSIDER:

Prediction Is Everywhere

We first introduced the term "prediction" in Chapter 5, "Perceiving Objects and Scenes," when we discussed how the Gestalt laws of organization predict what we will perceive in certain situations. But the history of prediction in perception really began with Helmholtz's theory of unconscious inference (p. 108). Helmholtz didn't use the word "prediction" when he proposed his theory, but think about what he proposed: We perceive the object that is *most likely* to have caused the image on the retina. In other words, perception of an object is based on a prediction about what's *probably* out there.

Prediction also appeared in Chapter 6, "Visual Attention," when we saw that people often direct their gaze to where they expect something is going to be (p. 131). Chapter 6 also introduced how the corollary discharge indicates where the eye is going to move next (p. 128). What makes this a prediction is that the CD occurs before the movement happens. The CD is saying, basically, "here's what's coming next." And luckily for us, that message helps keep our perception of the world stable, even as the moving eye creates a smeared image on the retina.

These examples of prediction from Chapters 5 and 6 have two things in common: (1) we are not usually conscious of their operation, and (2) they operate extremely rapidly—on a scale of fractions of a second. This rapid operation makes sense, because we see objects almost instantaneously, and because the eyes move very rapidly.

We also encountered prediction a number of times in this chapter, especially as we discussed dispensing the ketchup on that burger. The CD came into play again, as one of the sources of information that helps guide our reach and that helps calibrate our grip so it is strong enough to keep the bottle from slipping when we hit it.

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Prediction is also involved in some of the other things we discussed in this chapter, especially predicting other people's intentions, and how predictions about how to interact with the environment can be based on how difficult we think it will be to carry out a particular action.

Compared to the *object* and *eye movement* predictions described in Chapters 5 and 6, this chapter's *action* predictions occur on a longer time scale—seconds, rather than fractions of a second. Also, we can be conscious of making some predictions, such as when we're trying to predict how heavy an object is that we have to lift or when we are trying to determine someone else's intentions.

In the next chapter, we will consider how prediction (and our friend the CD) plays a role in perceiving motion, and later, we will see that prediction comes into play in the following chapters:

- Chapter 10, "Perceiving Depth and Size." Our perception of size is determined by our perception of its depth.
- Chapter 13, "Perceiving Music." Prediction is a central feature of music perception, because people expect a musical composition to unfold in a specific way. Sometimes, when unexpected notes or phrases occur, we can find the music jarring, or more interesting, depending on how much the music has deviated from what we were expecting.
- Chapter 14, "Perceiving Speech." Prediction is involved in our ability to perceive words, sentences, and stories. Prediction also influences how we perceive our own voices as we are speaking.
- Chapter 15, "Cutaneous Senses." Prediction influences our experience when we are touched, so touching yourself and being touched by someone else can feel different. This is one reason you can't tickle yourself!
- Chapter 16, "Chemical Senses." The fact that the experience of taste is influenced by what we were expecting to taste is demonstrated by strong reactions people experience when they think they are going to taste one thing, but something else happens instead.

From these examples, it is clear that prediction is a general phenomenon that occurs across many sensory modalities. One reason for this is adaptive: Knowing what is coming next can enhance survival. As we will see in the chapters that follow, prediction can not only let us know what's coming, but can shape the very nature of our perceptions.

DEVELOPMENTAL DIMENSION Infant Affordances

An infant exploring the environment by crawling (**Figure 7.30a**) sees the world from a low vantage point. But when the infant becomes older and is able to stand and walk, his view of the world changes (**Figure 7.30b**). These two situations have recently been studied by considering infant affordances. Remember that affordances were described by J. J. Gibson as *what it offers an animal, what it provides or furnishes* (p. 152). As we consider infant affordances, we will be considering what the environment offers infants in their quest to locomote through the environment, first by crawling, then by walking. Very young infants can't do much, so the range of possible affordances is relatively narrow. But as physical and motor development create new ways of interacting with the environment, new affordances for action open up.

Infants learn to crawl at about 8 months (range = 6–11 months) and to walk at about 12 months (range = 9–15 months) (Martorell et al., 2006). Compared with crawling, walking infants move more, go farther, travel faster, carry objects more frequently, and perhaps most important, enjoy an expanded field of view of the world (Adolph & Tamis-LeMonda, 2014). **Figure 7.31** shows how crawling infants mostly see the ground in front of their hands, but when infants stand

Figure 7.30 The infant's view of the world changes when the infant progresses from crawling to standing.

(a)

(b)

Joanna Oseman

Continued

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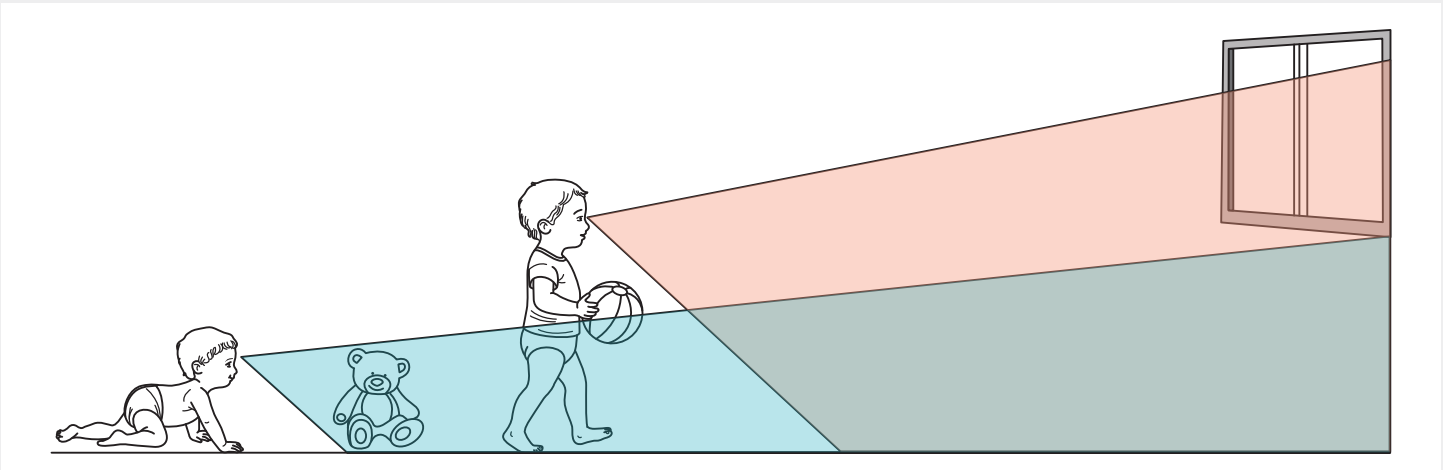

Figure 7.31 Infant crawling versus walking viewpoints. (Adolph, 2019)

on two feet and walk, the whole room swoops into view, creating new possibilities for seeing and doing (Adolph & Hoch, 2019; Kretch et al., 2014). Thus, as the infants develop new ways of locomoting, they gain new affordances for getting from one place to another.

Kari Kretch and Karen Adolph (2013) used the adjustable drop-off shown in **Figure 7.32** to test crawling and walking infants' ability to perceive affordances for locomotion. All of the babies were the same age (12 months), but half were experienced crawlers (mean = 18 weeks of crawling experience), and half had just begun walking (mean = 5 weeks of walking experience). The apparatus was adjusted in 1-cm increments to create drop-offs ranging from small (a navigable 1-cm "step") to large (an impossibly high 90 cm "cliff"). Infants began each trial facing the precipice—crawlers on hands and knees, and walkers upright. Caregivers stood at the bottom of the drop-off and encouraged infants to crawl or walk using toys and snacks as incentives. A highly trained experimenter followed alongside infants to catch them if they misperceived the affordances and fell.

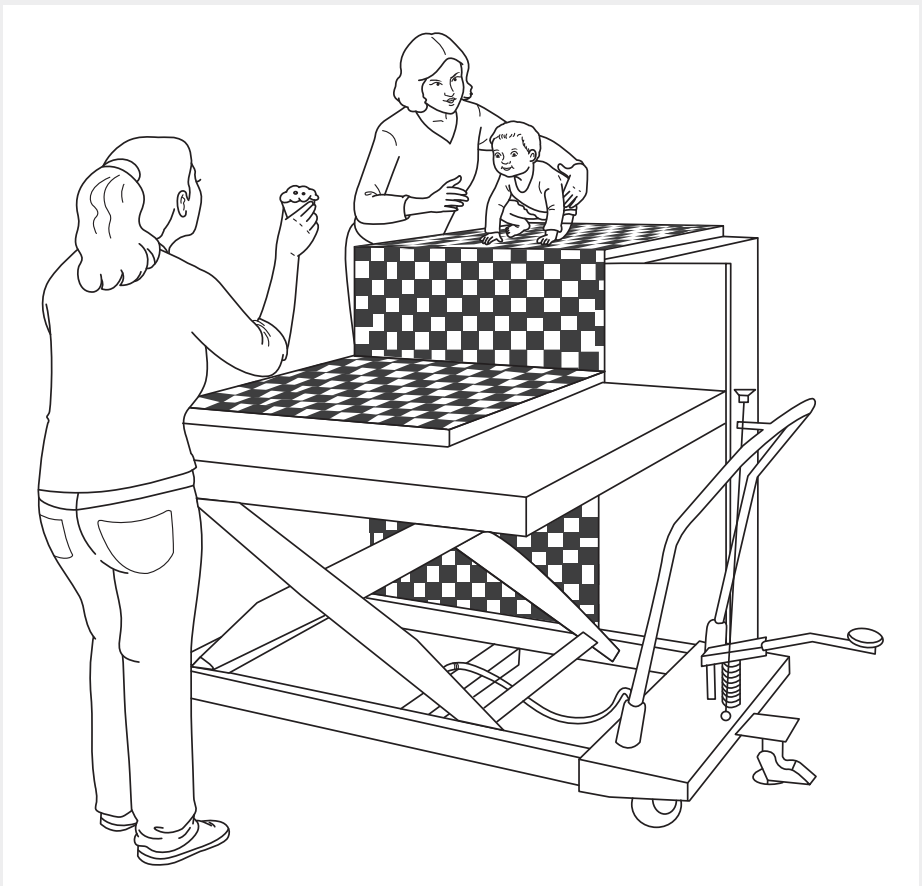

Figure 7.32 The adjustable drop-off apparatus used by Kretch and Adolph (2013). Infants were tested on drop-offs ranging from 1 cm to 90 cm. The 90-cm cliff is shown here. (Kretch & Adolph, 2013)

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Every infant crawled or walked over the small, 1-cm drop-off. But experienced crawlers and novice walkers behaved very differently on larger drop-offs. The experienced crawlers only attempted to crawl over drop-offs within their ability. When drop-offs were beyond their ability, they stopped at the edge or scooted down backward feet first. None attempted to crawl over the 90-cm cliff. The novice walkers were a completely different story. They walked blithely over small and large drop-offs alike on trial after trial, regardless of the affordances. They even attempted to walk over the 90-cm drop-off on 50 percent of trials (so the experimenter had to catch them in mid-air).

What do these results mean? The novice walkers averaged only 5 weeks of walking experience, but before that, they had been experienced crawlers with about 16 weeks of crawling experience just like the experienced crawlers who had perceived affordances accurately and refused to crawl over a cliff-sized precipice. It would seem that all those weeks of crawling experience should teach infants to avoid locomotion over large drop-offs—regardless of whether they're crawling or walking. But it does not. After crawlers get up and begin to walk, they must relearn how to perceive affordances for their new upright posture, which creates a new, higher vantage point. And sure enough, at 18 months of age, after the once-novice walkers had acquired about 23 weeks of walking experience, they perceived affordances accurately again.

Just like experienced crawlers, experienced walkers only attempted to walk over drop-offs within their ability. They stopped at the edge of the 90-cm cliff on 100 percent of trials. Thus, crawling experience teaches infants to perceive affordances for crawling, and walking experience teaches infants to perceive affordances for walking. The body–environment relations for crawling and walking are completely different, the information-gathering behaviors and vantage point are different, so learning from the earlier developing skill does not transfer to the later developing skill.

Another aspect of infant affordances in addition to experience is planning. Infants must perceive what's coming up *before* it happens, so they can adjust their behavior accordingly. Simone Gil and coworkers (2009) demonstrated that infants learned to plan their actions ahead of time when walking down slopes that varied in steepness, from 0 degrees to 50 degrees in 2-degree increments (**Figure 7.33a**). In infants' first weeks of walking they "march straight over the brink of impossibly steep slopes, requiring rescue by an experimenter" (p. 1). But with each week of walking experience, infants become better able to distinguish the affordances of shallow versus steep slopes and to adjust their walking behavior accordingly.

Figures 7.33b and **7.33c** show the footprints of an experienced infant approaching a shallow slope and a steep slope. The infant took long, evenly spaced steps while walking down the shallow 6-degree slope, but took bunched-up steps before she stepped over the steep 24-degree slope. These bunched-up steps show that the infant had predicted what was coming up and then took appropriate action to deal with it. So just as adults adjust their hand while reaching for a bottle to match the bottle's shape in anticipation of grasping it, infants modify their steps while approaching a slope to match the degree of slant in anticipation of walking on the slanted surface.

The message from these experiments is clear: The next time you see a baby crawling or walking, remember they're not just moving their arms and legs. They're acquiring new ways to interact with the environment, and they're learning to perceive and exploit affordances for action.

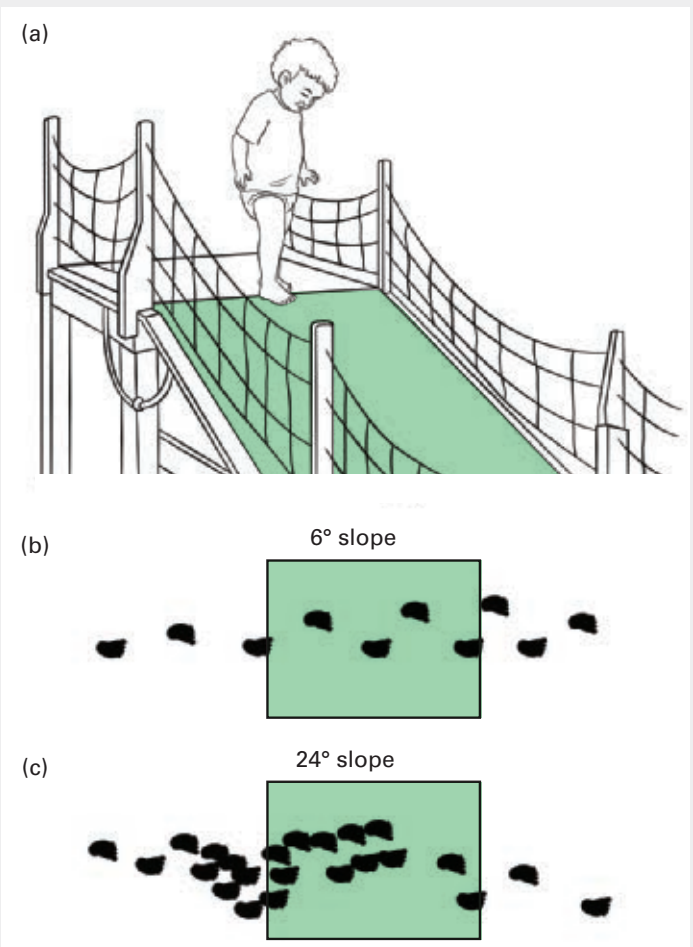

Figure 7.33 (a) An infant deciding whether to descend a slope. (b) Footprints indicating walking pattern for a 6-degree slope. (c) Footprints for the steeper 24-degree slope. (From Adolph, 2019)

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TEST YOURSELF 7.2

1. Why is a scene perceived as stationary, even though its image moves across the retina during an eye movement?
2. What is the corollary discharge?
3. How does the idea of *what* (ventral) and *how* (dorsal) streams help us describe an action such as reaching for a ketchup bottle?
4. What is the parietal reach region? Describe Fattori's experiments on "grasping neurons."
5. What is proprioception? What happened to Ian Waterman?
6. What are three sources of information for the position of the hand and arm during reaching?
7. How does disrupting the corollary discharge affect reaching behavior?
8. Describe the size-weight illusion. What does it tell us about how expectations affect lifting?
9. Describe what happens to the person's grip on the ketchup bottle when (a) they hit the bottle with their other hand, and (b) when someone else hits the bottle. Why is there a difference?
10. What are mirror neurons? What is the evidence that mirror neurons aren't just responding to a specific pattern of motion?
11. Is there any evidence that there are mirror neurons in the human brain?
12. Describe Iacoboni's experiment that suggested there are mirror neurons that respond to intentions.
13. What is a possible mechanism that might be involved in mirror neurons that respond to intentions?
14. What are some of the proposed functions of mirror neurons? What is the scientific status of these proposals?
15. Describe the action-based account of perception. In your discussion, indicate (a) why some researchers think the brain evolved to enable us to take action and (b) how experiments have demonstrated a link between perception and "ability to act."
16. What is the evidence behind the statement that "prediction is everywhere"?
17. What is an example of an affordance, as applied to young infants? What is the evidence that infants develop affordances? What do infant stepping patterns tell us about their affordances?

THINK ABOUT IT

1. We have seen that gymnasts appear to take visual information into account as they are in the act of executing a somersault. In the sport of synchronized diving, two people execute a dive simultaneously from two side-by-side diving boards. They are judged based on how well they execute the dive and how well the two divers are synchronized with each other. What environmental stimuli do you think synchronized divers need to take into account in order to be successful?
2. Can you identify specific environmental information that you use to help you carry out actions in the environment? This question is often particularly relevant to athletes.
3. It is a common observation that people tend to slow down as they are driving through long tunnels. Explain the possible role of optic flow in this situation.
4. If mirror neurons do signal intentions, what does that say about the role of top-down and bottom-up processing in determining the response of mirror neurons?
5. How do you think the response of your mirror neurons might be affected by how well you know a person whose actions you were observing?
6. How does your experience in interacting with the environment (climbing hills, playing sports) correspond or not correspond to the findings of the "potential for action" experiments described in the Something to Consider section?

KEY TERMS

Action affordance (p. 154)
Action-specific perception hypothesis (p. 168)
Affordances (p. 152)
Audiovisual mirror neurons (p. 165)
Cognitive map (p. 157)
Ecological approach to perception (p. 150)
Focus of expansion (FOE) (p. 151)
Gradient of flow (p. 150)
Grid cells (p. 157)
Invariant information (p. 151)
Landmark (p. 156)
Mirror neurons (p. 164)
Mirror neuron system (p. 165)
Optic flow (p. 150)
Parietal reach region (PRR) (p. 160)
Place cells (p. 157)
Place field (p. 157)
Proprioception (p. 162)
Size-weight illusion (p. 162)
Spatial updating (p. 155)
Visual direction strategy (p. 154)
Visuomotor grip cells (p. 162)
Wayfinding (p. 155)

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We perceive motion when images move across our retina, as would occur if these birds flew across our field of view; when we move our eyes to follow the birds' movements; and when we are influenced by knowledge we have gained from perceiving motion in the past.

Ashley Cooper/Getty Images

Learning Objectives

After studying this chapter, you will be able to ...

- Describe five different functions of motion perception.
- Understand the difference between real motion and illusory motion and what research has revealed about the relation between them.
- Describe how we perceive motion both when we move our eyes to follow a moving object and when we keep our eyes steady as an object moves across our field of view.
- Understand the multiple neural mechanisms that explain motion perception.
- Describe why we need to go beyond considering the responses of single neurons to understand the physiology of motion perception.
- Understand how perceiving movement of the body has been studied both behaviorally and physiologically.
- Describe what it means to say that we can perceive motion in still pictures.
- Describe how infants perceive biological motion.

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CHAPTER 8

Perceiving Motion

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TEST YOURSELF 8.1

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SOMETHING TO CONSIDER: Motion, Motion, and More Motion

DEVELOPMENTAL DIMENSION: Infants Perceive Biological Motion

TEST YOURSELF 8.2

THINK ABOUT IT

Some Questions We Will Consider:

- Why do some animals freeze in place when they sense danger? (p. 176)
- How do films create movement from still pictures? (p. 179)
- What's special about movement of human and animal bodies? (p. 188)

Perhaps the most dramatic way to illustrate the importance of motion perception to daily life (and survival) comes from case studies of people who, through disease or trauma, suffer from damage to parts of the brain responsible for perceiving and understanding movement. When this happens, a person is said to suffer from a condition called akinetopsia or "motion blindness," where motion is either very difficult or impossible to perceive. The most famous and well-studied case of akinetopsia is a 43-year-old woman known as L.M. (Zihl et al., 1983, 1991).

Without the ability to perceive motion following a stroke, L.M. was unable to successfully complete activities as simple as pouring a cup of tea. As she put it, "the fluid appeared to be frozen, like a glacier," and without the ability to perceive the tea rising in the cup, she had trouble knowing when to stop pouring. Her condition caused other, more serious problems as well. It was difficult for her to follow dialogue because she couldn't see the motions of a speaker's face and mouth, and people suddenly appeared or disappeared because she couldn't see them approaching or leaving. Crossing the street presented serious problems because at first a car might seem far away, but then suddenly, without warning, it would appear very near. Thus, her disability was not just a social inconvenience but enough of a threat to the woman's well-being that she rarely ventured outside into the world of moving—and sometimes dangerous—objects.

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8.1 Functions of Motion Perception

The experience of L.M. and the few other people with akinetopsia makes it clear that being unable to perceive motion is a great handicap. But looking closely at what motion perception does for us reveals a long list of functions.

Detecting Things

Detection is at the head of the list because of its importance for survival. We need to detect things that might be dangerous in order to avoid them. Imagine, for example, that you are reading a book under your favorite tree on campus when a stray baseball flies in your general direction. Without thinking, your natural response is to look up from your book and quickly move out of the ball's path. This is an example of attentional capture, discussed in Chapter 6 (p. 130), in which our attention is automatically drawn to salient objects. Motion is a very salient aspect of the environment, so it attracts our attention (Franconeri & Simons, 2003).

Movement perception is extremely important for animals that hunt, because movement reveals prey which, when stationary, may be difficult to see because of camouflage (**Figure 8.1**), but which become visible if they move. Movement serves a similar purpose for the prey, who use movement to detect predators as they approach.

Or examining a less life-or-death function of movement perception, consider the problem of trying to find your friend among a sea of faces in the stadium. Looking up at the crowd, you have no idea where to look, but suddenly you see a person waving and recognize that it is your friend. The detection function of movement perception comes to the rescue!

Perceiving Objects

Movement helps us perceive objects in a number of ways. Remembering our discussion from Chapter 5 (p. 91) about how even clearly visible objects may be ambiguous, you can appreciate how motion of an object can reveal characteristics that might not be obvious from a single, stationary view (**Figure 8.2a**). Movement of an observer around an object can have a similar effect: Viewing the "horse" in **Figure 8.2b** from different perspectives reveals that its shape is not exactly what you may have expected based on your initial view. Thus, our own motion relative to objects is constantly adding to the information we have about those objects, and, most relevant to this chapter, we receive similar information when objects move relative to us. Observers perceive shapes more rapidly and accurately when an object is moving (Wexler et al., 2001).

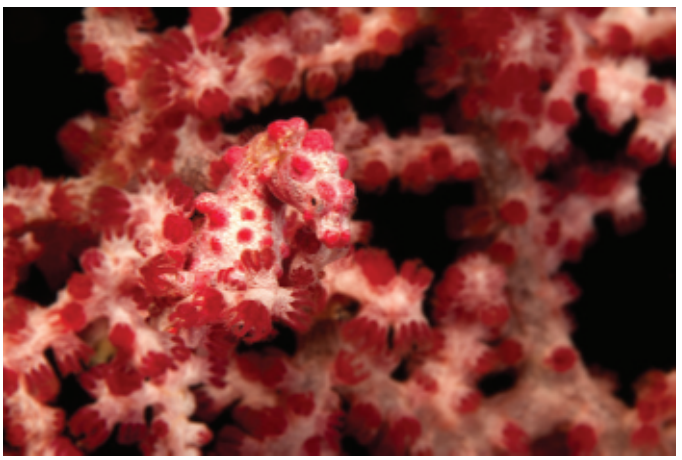
Movement also serves an organizing function, which groups smaller elements into larger units. The motion of individual birds becomes perceived as the larger unit of the flock, in which the birds are flying in synchrony with each other. When a person or animal moves, movement of individual units—arms, legs, and body—become coordinated with each other to create a special type of movement called biological movement, which we will discuss later in the chapter.

Perceiving Events

As we observe what's going on around us, we typically observe ongoing behavior as a sequence of events. For example, consider events that might occur in a coffee shop. You observe a man enter the shop, stop at the counter, have a brief conversation with the barista, who in turn leaves and returns with coffee in a paper cup. The customer pushes down on the lid to make sure it is secure, pays for the coffee, drops a tip into the tip jar, turns around, and walks out the door.

Ashley Cooper/Getty Images

(a)



Stephen Frink/Getty Images

(b)

Figure 8.1 Even perfectly camouflaged animals like this (a) leaf-tail gecko and (b) pygmy sea horse would be instantly revealed by their movement.

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(a)

(b)

Bruce Goldstein

Figure 8.2 (a) The shape and features of this car are revealed when different aspects of it become visible as it moves. (b) Moving around this "horse" reveals its true shape.

This description, which represents only a small fraction of what is happening in the coffee shop, is a sequence of events unfolding in time. And just as we can segment a static scene into individual objects, we can segment ongoing behavior into a sequence of events, where an **event** is defined as a segment of time at a particular location that is perceived by observers to have a beginning and an end (Zacks & Tversky, 2001; Zacks et al., 2009).

In our coffee shop scenario, placing an order with the coffee barista is an event, reaching out to accept the cup of coffee is an event, dropping change in the tip jar is an event, and so on. The point in time when each of these events ends and the next one begins is called an **event boundary**. The connection of events to motion perception becomes obvious when we consider that event boundaries are often associated with changes in the nature of motion. One pattern of motion occurs when placing the order, another when reaching out for the coffee cup, and so on.

Jeffrey Zacks and coworkers (2009) measured the connection between events and motion perception by having participants watch films of common activities such as paying bills or washing dishes and asking them to press a button when they believe one unit of meaningful activity ended and another began (Newtson & Engquist, 1976; Zacks et al., 2001). When Zacks compared event boundaries to the actor's body movements measured with a motion tracking system, he found that event boundaries were more likely to occur when there was a change in the speed or acceleration of the actor's hands. From the results of this and other experiments, Zacks concluded that the perception of movement plays an important role in separating activities into meaningful events.

Social Perception

Interactions with other people involve movement at many levels. L.M.'s akinetopsia made it difficult for her to interact with people, because she couldn't tell who was talking by seeing their lips moving. On a larger scale, we use movement cues to determine a person's intentions. If you see someone across the street waving an arm, are they hailing a taxi or swatting at a fly? An experiment by Atesh Koul and coworkers (2019) showed that the speed and timing of the movement can help answer this type of question. In their experiment, they had participants observe a hand reaching for a bottle, with the intention of either drinking or pouring from it, and were asked to indicate, "pour" or "drink." When the experimenter compared motion information such as the velocity and trajectory of the hand, and the nature of the grip, to the participant's judgments, they found that participants were using this information to decide why the hand was reaching for the cup (also see Cavallo et al., 2016).

Other experiments have shown that the characteristics of movement can be used to interpret emotions (Melzer et al., 2019). The link between motion intention and emotion is so powerful that it can give human characteristics to geometrical objects. This was demonstrated in a famous experiment by Fritz Heider and Marianne Simmel (1944), who showed a 2½-minute animated film to participants and asked them to describe what was happening in the movie. The movie consisted of a "house" and three "characters"—a small circle, a small triangle, and a large triangle. These three geometric objects moved around both inside and outside the house, and sometimes interacted with each other (**Figure 8.3**).

Although the characters in the film were geometric objects, the participants created stories to explain the objects' actions, often giving them humanlike characteristics and personalities. For example, one account described the small triangle and circle as a couple who were trying to be alone in the house when the big triangle ("a bully") entered the house and interrupted them. The small triangle didn't appreciate this intrusion and attacked the big triangle. In other studies, researchers have shown how such simple motion displays can evoke interpretations of desire, coaxing, chasing, fighting, mocking, fearfulness, and seduction (Abell et al., 2000; Barrett et al., 2005; Castelli et al., 2000; Csibra, 2008; Gao et al., 2009). Who would have thought the world of geometric objects could be so exciting?

Although assigning social motives to moving geometrical objects makes a great story, the real story occurs as we interact

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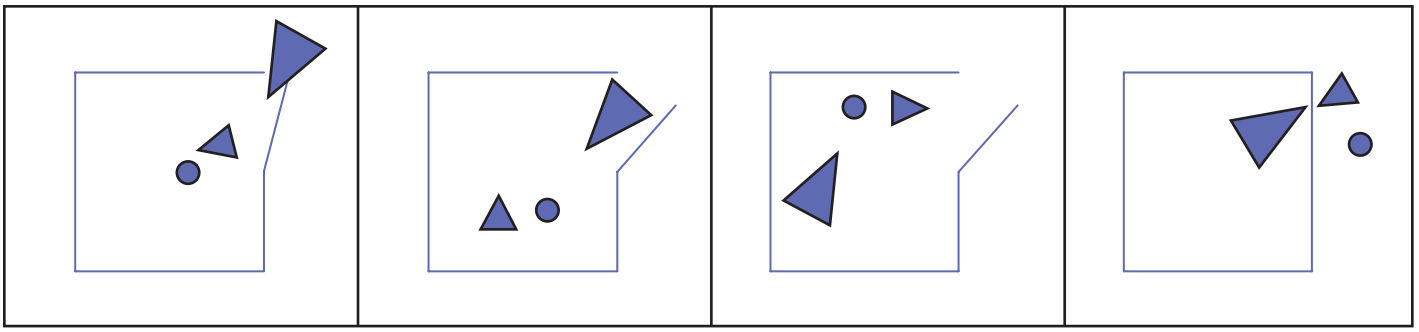

Figure 8.3 Still images from a film like one used by Heider and Simmel (1944). The objects moved in various ways, going in and out of the "house" and sometimes interacting with each other. The nature of the movements led participants to make up stories that often described the objects as having feelings, motivations, and personalities.

with people in social situations. Many social cues are available in person-to-person interactions, including facial expressions, language, tone of voice, eye contact, and posture, but research has shown that movement can provide social information even when these other cues aren't available.

For example, Laurie Centelles and coworkers (2013) used a way of presenting human motion called **point-light walkers**, which are created by placing small lights on people's joints and then filming the patterns created by these lights when people move (Johansson, 1973, 1975; **Figure 8.4**). When a person wearing the lights moves, observers see a "person moving" without any of the other cues that can occur in social situations. The observers in Centelles' experiment viewed the stimulus created by two people wearing lights under two conditions: (1) social interaction: the people were interacting in various ways and (2) non-social interaction: the people were near each other but were acting independently.

The observers were able to indicate whether the two people were interacting with each other or were acting independently. Interestingly, a group of observers with autism spectrum disorder, which is characterized by having difficulty with real-life social interactions, were not as good as the other observers at telling the difference between the social and non-social conditions. Many other studies have shown that movement provides information that facilitates social interactions (Barrett et al., 2005; Koppensteiner, 2013).

Taking Action

Our discussion in Chapter 7, "Taking Action," was full of movement. Navigating ourselves through the environment and walking down a crowded sidewalk are examples of how our own movement depends on our perception of movement. We perceive the stationary scene moving past us as we walk down the sidewalk. We pay attention to other people's movements to avoid colliding with them.

Movement perception is also crucially involved in sports—both watching, as you follow a double-play unfold in baseball or watch the trajectory of a long pass in football, or as you participate yourself.

Finally, let's return to picking up the ketchup bottle we discussed in Chapter 7 (see Figure 7.17). Each component of our action—reaching for the bottle, grasping it, lifting it—generates motion that we must keep track of in order to get the ketchup onto the burger.

From the discussion above, it is clear that perceiving motion is involved in our lives at many levels: detecting stimuli, perceiving objects, understanding events, interacting socially with others, and carrying out physical actions ranging from walking down the sidewalk, to watching sports, to reaching for a bottle of ketchup. We now consider how researchers have gone about studying motion perception.

Figure 8.4 Point light walker stimulus created by placing lights on a person and having them walk in the dark. In the experimental situation, only the lights and their motion are visible.

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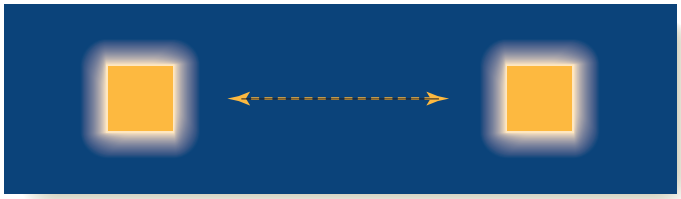
8.2 Studying Motion Perception

A central question in the study of motion perception is, *when do we perceive motion?*

When Do We Perceive Motion?

The answer to this question may seem obvious: We perceive motion when something moves across our field of view, which is an example of **real motion**. Perceiving a car driving by, people walking, or a bug scurrying across a tabletop are all examples of the perception of real motion. However, there are three types of **illusory motion**—the perception of the motion of stimuli that aren't actually moving.

Apparent motion is the most famous and most studied type of illusory motion. We introduced apparent motion in Chapter 5 when we told the story of Max Wertheimer's observation that when two stimuli in slightly different locations are alternated with the correct timing, an observer perceives one stimulus moving back and forth smoothly between the two locations (**Figure 8.5a**; also see Figure 5.12).



(a) Flash Dark Flash

Bruce Goldstein

(b)

Figure 8.5 Apparent motion (a) between two lights, which appear to move back and forth when they are rapidly flashed one after the other; (b) on a moving sign. Our perception of words moving across a lighted display is so compelling that it is often difficult to realize that signs like this are simply lights flashing on and off.

This perception is called apparent motion because there is no actual (or real) motion between the stimuli. This is the basis for the motion we perceive in movies, on television, and in moving signs that are used for advertising and entertainment (**Figure 8.5b**).

Induced motion occurs when motion of one object (usually a large one) causes a nearby stationary object (usually smaller) to appear to move. For example, the moon usually appears stationary in the sky. However, if clouds are moving past the moon on a windy night, the moon may appear to be racing through the clouds. In this case, movement of the larger object (clouds covering a large area) makes the smaller, but actually stationary, moon appear to be moving.

Motion aftereffects occur when viewing a moving stimulus causes a stationary stimulus to appear to move (Glasser et al., 2011). One example of a motion aftereffect is the **waterfall illusion** (Addams, 1834) (**Figure 8.6**). If you look at a waterfall for 30 to 60 seconds (be sure it fills up only part of

Dennis Barnes/Britain On View/Getty Images

Figure 8.6 An image of the Falls of Foyers near Loch Ness in Scotland where Robert Addams (1834) first experienced the waterfall illusion. Looking at the downward motion of the waterfall for 30 to 60 seconds can cause a person to then perceive stationary objects such as the rocks and trees that are off to the side as moving upward.

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your field of view) and then look off to the side at part of the scene that is stationary, you will see everything you are looking at—rocks, trees, grass—appears to move upward for a few seconds. If you're short on waterfalls, next time you are at the movies, you may be able to induce this illusion by carefully watching the rolling credits at the end of the movie and then looking off to the side. This works best if you sit toward the rear of the theater.

Researchers studying motion perception have investigated all the types of perceived motion described above—and a number of others as well (Blaser & Sperling, 2008; Cavanaugh, 2011). Our purpose, however, is not to understand every type of motion perception but to understand some of the principles governing motion perception in general. To do this, we will focus on real and apparent motion.

Comparing Real and Apparent Motion

For many years, researchers treated the apparent motion created by flashing stationary objects or pictures and the real motion created by actual motion through space as though they were separate phenomena, governed by different mechanisms. However, there is ample evidence that these two types of motion have much in common. For example, Axel Larsen and coworkers (2006) presented three types of displays to a person in an fMRI scanner: (1) a *control condition*, in which two squares in slightly different positions were flashed simultaneously (**Figure 8.7a**); (2) a *real motion display*, in which a small square moved back and forth (**Figure 8.7b**); and (3) an *apparent motion display*, in which squares were flashed one after another so that they appeared to move back and forth (**Figure 8.7c**).

Larsen's results are shown below the dot displays. The blue-colored area in Figure 8.7a is the area of visual cortex activated by the control squares, which are perceived as two squares simultaneously flashing on and off with no motion between them. Each square activates a separate area of the cortex. In Figure 8.7b, the red indicates the area of cortex activated by real movement of the square. In Figure 8.7c, the yellow indicates the area of cortex activated by the apparent motion display. Notice that the activation associated with apparent motion is similar to the activation for the real motion display. Two flashed squares that result in apparent motion activate the area of the brain representing the space between the positions of the flashing squares even though no stimulus is presented there.

Because of the similarities between the neural responses to real and apparent motion, researchers study both types of motion together and concentrate on discovering general mechanisms that apply to both. In this chapter, we will follow this approach as we look for general mechanisms of motion perception. We begin by describing two real-life situations in which we perceive motion.

Two Real-Life Situations We Want to Explain

Figure 8.8a shows a situation in which Jeremy is walking from left to right and Maria is following Jeremy's motion with her eyes. In this case, Jeremy's image remains stationary on Maria's retinas, yet Maria perceives Jeremy as moving. This means that motion perception can't be explained just by the motion of an image across the retina.

Figure 8.8b shows a situation in which Maria looks straight ahead as Jeremy walks by. Because she doesn't move her eyes, Jeremy's image sweeps across her retina. Explaining motion perception in this case seems straightforward because as Jeremy's image moves across Maria's retina, it stimulates a series of receptors one after another, and this stimulation signals Jeremy's motion.

In the sections that follow, we will consider a number of different approaches to explaining motion perception when (1) the eye is moving to follow an object as it moves (Figure 8.8a), and (2) the eye is stationary as an object moves across the visual field (Figure 8.8b). We begin by considering an approach based on J. J. Gibson's ecological approach to perception that we described in Chapter 7 (p. 150).

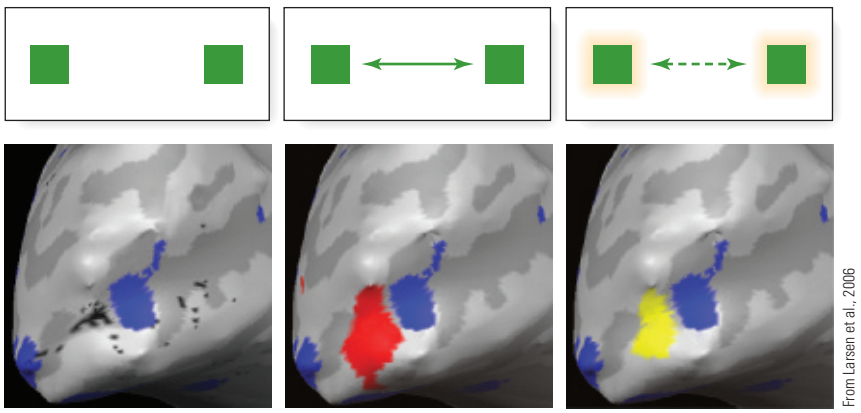

Figure 8.7 Three conditions in Larsen's (2006) experiment: (a) control condition, in which two squares in slightly different positions were flashed simultaneously; (b) real motion, in which a small square moved back and forth; (c) apparent motion, in which squares were flashed one after another so that they appeared to move back and forth. Stimuli are shown on top and the resulting brain activation is shown below. In (c), the brain is activated in the space that represents the area between the two dots, where movement was perceived but no stimulus was present.

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(a) Jeremy walks past Maria; Maria follows him with her eyes (creates local disturbance in optic array)

(b) Jeremy walks past Maria; Maria's eyes are stationary (creates local disturbance in optic array)

(c) Scans scene by moving her eyes from left to right (creates global optic flow)

Figure 8.8 Three motion situations. (a) Maria follows Jeremy's movement with her eyes. (b) Maria is stationary and looks straight ahead as Jeremy walks past. (c) Maria moves her eyes from left to right.

8.3 The Ecological Approach to Motion Perception

Gibson's approach (1950, 1966, 1979), which we introduced in Chapter 7, involves looking for information in the environment that is useful for perception (see page 150). This information for perception, according to Gibson, is located not on the retina but "out there" in the environment. He thought about information in the environment in terms of the **optic array**—the structure created by the surfaces, textures, and contours of the environment—and he focused on how movement of the observer causes changes in the optic array. Let's see how this works by returning to Jeremy and Maria in Figure 8.8.

In Figure 8.8a, when Jeremy walks from left to right and Maria follows him with her eyes, portions of the optic array become covered as he walks by and then are uncovered as he moves on. This result is called a **local disturbance in the optic array**. This local disturbance in the optic array, which occurs when Jeremy moves relative to the environment, covering and uncovering the stationary background, causes Maria to perceive Jeremy's movement, even though his image is stationary on her retina.

In Figure 8.8b, when Maria keeps her eyes still as Jeremy walks past, Jeremy's image is moving across her retina, but as far as Gibson is concerned, the crucial information for movement is the same local disturbance in the optic array that occurred when Maria was keeping her eyes still. Whether Maria's eyes are moving or still, the local disturbance out there in the environment signals that Jeremy is moving.

Gibson's approach explains not only why Maria perceives movement in the situations in Figures 8.8a and 8.8b, but also why she doesn't perceive movement when she moves her eyes across the stationary scene. The reason is that as Maria moves her eyes from left to right, everything around her—the walls, the window, the trash can, the clock, and the furniture—moves to the left of her field of view (**Figure 8.8c**). A similar situation would occur if Maria were to walk through the scene. The fact that everything moves at once in response to movement of the observer's eyes or body is called **global optic flow**; this signals that the environment is stationary and that the observer is moving, either by moving their body or by scanning with their eyes, as in this example. Thus, according to Gibson, motion is perceived when one part of the visual scene moves relative to the rest of scene, and no motion is perceived when the entire field moves, or remains stationary. While this is a reasonable explanation, we will see in the next section that we also need to consider other sources of information to fully understand how we perceive motion in the environment.

8.4 The Corollary Discharge and Motion Perception

Gibson's approach focuses on information that is "out there" in the environment. Another approach to explaining the movement situations in Figure 8.8 is to consider the neural signals that travel from the eye to the brain. This brings us back to the **corollary discharge signal**, which we introduced in Chapter 6 (p. 128) to explain why we don't see the scene blur when we move our eyes from place to place when scanning a scene. We now consider how the corollary discharge comes into play as we perceive movement.

As we noted in Chapter 6, **corollary discharge theory** distinguishes three signals: (1) the **image displacement signal**, which occurs when an image moves across the retina, (2) the **motor signal**, which is sent from the motor area to the eye muscles to cause the eye to move, and (3) the corollary discharge signal, which is a copy of the motor signal. According to corollary discharge theory, movement will be perceived if a brain structure called the **comparator** (actually a number of brain structures) receives just one signal—either

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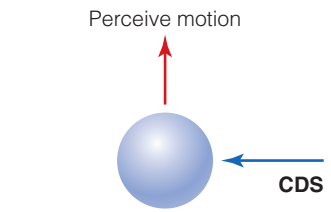
the image displacement signal or the corollary discharge signal. It also states that no movement will be perceived if the comparator receives both signals at the same time. Keeping that in mind, let's consider how corollary discharge theory would explain the perception that occurs in each of the situations in Figure 8.8.

Figure 8.9a shows the signals that occur when Maria is following Jeremy with her eyes. There is a CD signal, because Maria is moving her eyes. There is, however, no image displacement signal, because Jeremy's image stays in the same place on Maria's retina. The comparator, therefore, receives just one signal, so Maria perceives Jeremy to be moving.

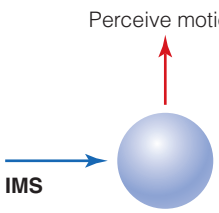
Figure 8.9b shows that if Maria keeps her eyes stationary as Jeremy walks across her field of view, there is an image movement signal, because Jeremy's image is moving across Maria's retina, but there is no CD signal, because Maria's eyes are not moving. Because only one signal reaches the comparator, movement is perceived.

Figure 8.9c shows that if Maria scans the room, there is a CD signal because her eyes are moving and an image movement signal because the scene is moving across her retinas. Because both signals reach the comparator, no movement is perceived. (Something to think about: How would this way of thinking about the CD apply to the situation described on page 129 of Chapter 6, which explains why people don't see a smeared image as the eye moves from the finger to the ear)

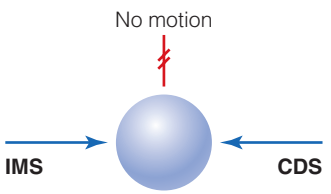
This situation has also been approached physiologically in another way, by focusing on how the moving image stimulates one retinal receptor after the other. We will describe this approach by first considering a neural circuit called the Reichardt detector.



(a) Eye follows moving stimulus.



(b) Eye is stationary; stimulus is moving.



(c) Eye moves across stationary scene.

Figure 8.9 According to the corollary discharge model, (a) when the CDS reaches the comparator alone, motion is perceived. (b) When the IMS reaches the brain alone, motion is also perceived. (c) If both the CDS and IMS reach the comparator together, they cancel each other, so motion is not perceived.

TEST YOURSELF 8.1

1. Describe five different functions of motion perception.
2. What is an event? What is the evidence that motion helps determine the location of event boundaries? What is the relation between events and our ability to predict what is going to happen next?
3. Describe four different situations that can result in motion perception. Which of these situations involves real motion, and which involve illusions of motion?
4. What is the evidence for similar neural responding to real motion and apparent motion?
5. Describe Gibson's ecological approach to motion perception. What is the advantage of this approach? (Explain how the ecological approach explains the situations in Figure 8.8.)
6. Describe how corollary discharge theory explains movement perception observed in Figures 8.8a and 8.8b.

8.5 The Reichardt Detector

We are now going to explain motion perception that occurs in Figure 8.9b, when movement is viewed by a stationary eye, by considering the neural circuit in **Figure 8.10**, proposed by Werner Reichardt (1961, 1987), which is called the **Reichardt detector**.

The Reichardt detector circuit consists of two neurons, A and B, which send their signals to an **output unit** that compares the signals it receives from neurons A and B. The key to the operation of this circuit is the **delay unit** that slows down the signals from A as they travel toward the output unit. In addition, the output unit has an important property: It multiplies the responses from A and B to create the movement signal that results in the perception of motion.

Let's now consider how this circuit responds as Jeremy, whose position is indicated by the red dot, moves from left to right. **Figure 8.10a** shows that Jeremy, approaching from the left, first activates neuron A. This is represented by the "spikes" shown in record 1. This response starts traveling toward the output unit, but is slowed by the delay unit. During this delay, Jeremy continues moving and stimulates neuron B (**Figure 8.10b**), which also sends a signal down to the output unit (record 2). If the timing is right, the delayed signal from A (record 3) reaches the output unit just when the signal from B (record 2) arrives. Because the output unit multiplies

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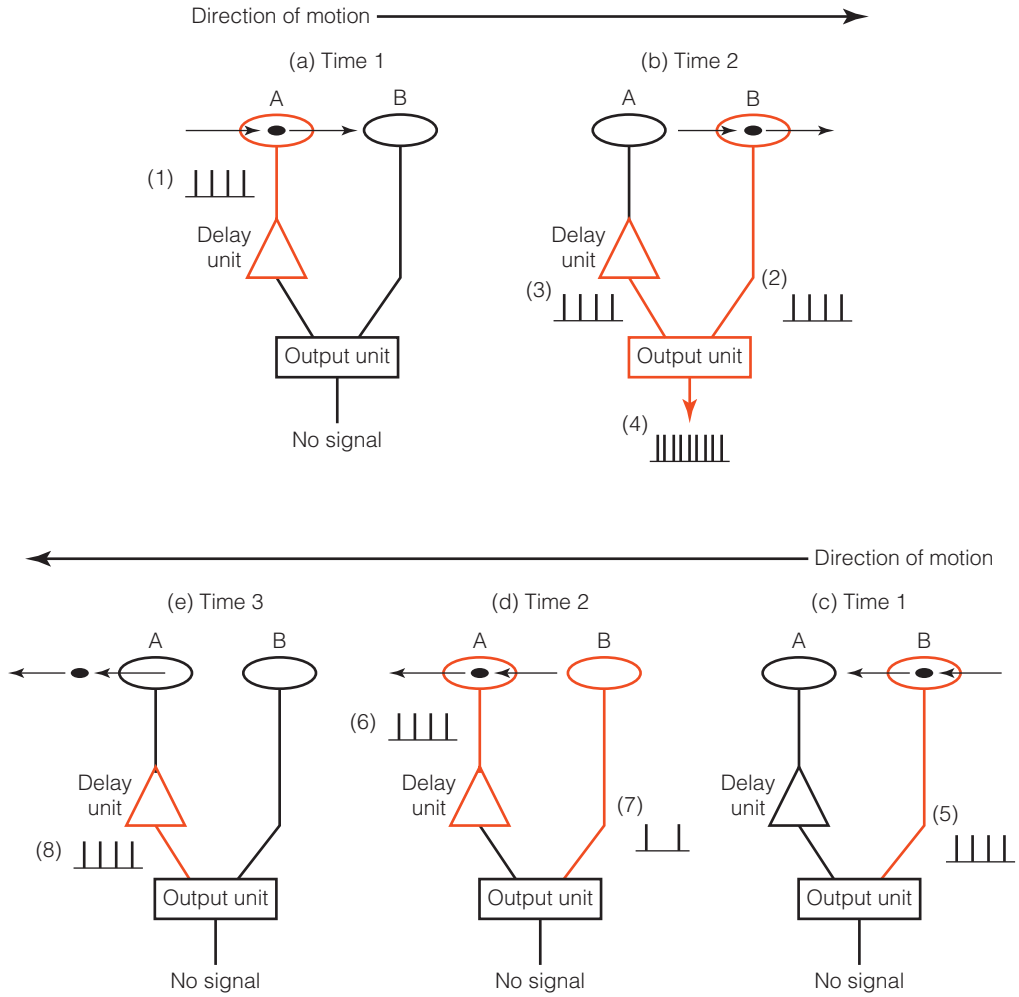

Figure 8.10 The Reichardt detector. Activated structures are indicated by red. The output unit creates a signal only if the signals from A and B reach it simultaneously. Top: Movement to the right results in a signal from the output unit. Bottom: Movement to the left results in no signal. See text for details.

the responses from A and B, a large movement signal results (record 4). Thus, when Jeremy moves from left to right at the right speed, a movement signal occurs and Maria perceives Jeremy's movement.

An important property of the circuit diagrammed in Figure 8.10 is that it creates a movement signal in response to movement from left to right, but does not create a signal for movement from right to left. We can see why this is so by considering what happens when Jeremy walks from right to left. Approaching from the right (**Figure 8.10c**), Jeremy first activates neuron B, which sends its signals directly to the output unit (record 5). Jeremy continues moving and activates neuron A (**Figure 8.10d**), which generates a signal (record 6). At this point, the response from B has become smaller because it is no longer being stimulated (record 7), and by the time the response from A passes through the delay unit and reaches the output unit, the response from B has dropped to zero (**Figure 8.10e**). When the output unit multiplies the delayed signal from neuron A and the zero signal from neuron B, the result is zero, so no movement signal is generated.

More complicated versions of this circuit, which have been discovered in amphibians, rodents, primates, and humans (Borst & Egelhaaf, 1989), create directionally sensitive neurons, which fire only to a particular direction of motion. The visual system contains many circuits like this, each tuned to a different direction of motion; working together, they can create signals that indicate the direction of movement across the visual field.

8.6 Single-Neuron Responses to Motion

The Reichardt detector is a neural circuit that creates a neuron that responds to movement in a specific direction. Such directionally-selective neurons were recorded from neurons in the rabbit's retina by Horace Barlow and coworkers (1964) and from neurons in the cat's visual cortex by David Hubel and Thorsten Wiesel (1959, 1965). Hubel and Wiesel's motion detecting neurons are the complex cells described in Chapter 4, which respond to movement in a particular direction (p. 70).

While the visual cortex is therefore important for motion perception, it is only the first in a series of many brain regions that are involved (Cheong et al., 2012; Gilaie-Dotan, et al., 2013). We will focus on the **middle temporal (MT) area** (see Figure 7.18, page 160), which contains many directionally

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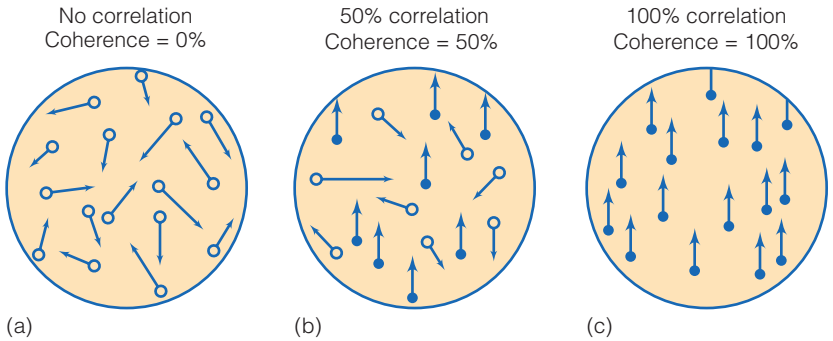

Figure 8.11 Moving dot displays used by Britten and coworkers (1992). These pictures represent moving dot displays that were created by a computer. Each dot survives for a brief interval (20–30 msec), after which it disappears and is replaced by another randomly placed dot. Coherence is the percentage of dots moving in the same direction at any point in time. (a) Coherence = 0 percent. (b) Coherence = 50 percent. (c) Coherence = 100 percent. (Adapted from Britten et al., 1992)

selective neurons. Evidence that the MT cortex is specialized for processing information about motion comes from experiments that have used moving dot displays in which the direction of motion of individual dots can be varied.

Experiments Using Moving Dot Displays

Figure 8.11a represents a display in which an array of dots are moving in random directions. William Newsome and coworkers (1995) used the term **coherence** to indicate the degree to which the dots move in the same direction. When the dots are all moving in random directions, coherence is 0 percent. **Figure 8.11b** represents a coherence of 50 percent, as indicated by the darkened dots, which means that at any point in time half of the dots are moving in the same direction. **Figure 8.11c** represents 100 percent coherence, which means that all of the dots are moving in the same direction.

Newsome and coworkers used these moving dot stimuli to determine the relationship between (1) a monkey's ability to judge the direction in which dots were moving and (2) the response of a neuron in the monkey's MT cortex. They found that as the dots' coherence increased, two things happened: (1) the monkey judged the direction of motion more accurately, and (2) the MT neuron fired more vigorously. The monkey's behavior and the firing of the MT neurons were so closely related that the researchers could predict one from the other. For example, when the dots' coherence was 0.8 percent, the monkey was not able to judge the direction of the dots' motion and the neuron's response did not differ appreciably from its baseline firing rate. But increasing the coherence increased the monkey's ability to judge the direction of motion, and by 12.8 percent coherence—so, out of 200 moving dots, about 25 were moving in the same direction—the monkey judged the correct direction of movement on virtually every trial, and the MT neuron always fired faster than its baseline rate.

Newsome's experiment demonstrates a relationship between the monkey's perception of motion and neural firing in its MT cortex. What is especially striking about Newsome's experiment is that he measured perception and neural activity in the same monkeys. Returning to the perceptual process introduced in Chapter 1 (Figure 1.13, page 12), which is shown in **Figure 8.12**, we can appreciate that what Newsome has done is to measure relationship C: the physiology–perception relationship. This measurement of physiology and perception in the same organism completes our perceptual process triangle, which also includes relationship A: stimulus–perception—the connection between how stimuli are moving and what we perceive; and relationship B: stimulus–physiology—the

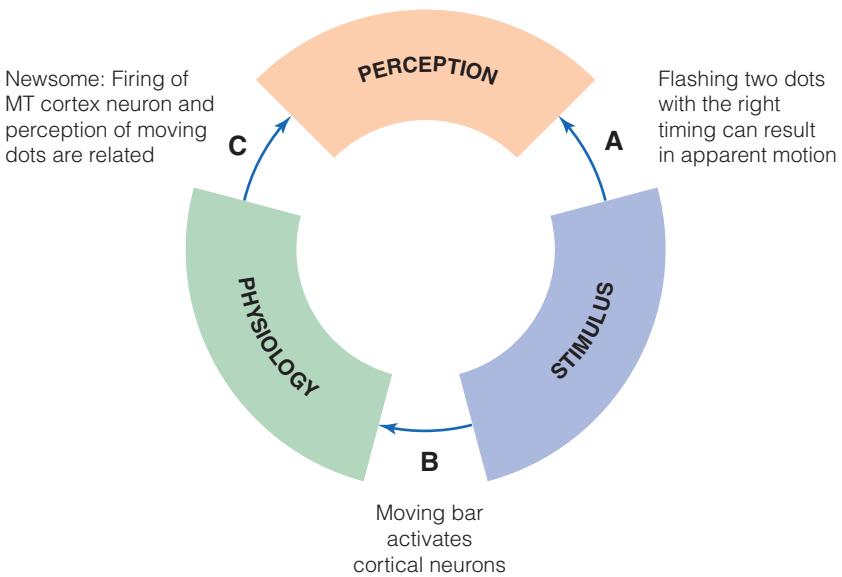
PERCEPTION
PHYSIOLOGY
STIMULUS
A
B
C
Newsome: Firing of MT cortex neuron and perception of moving dots are related
Flashing two dots with the right timing can result in apparent motion
Moving bar activates cortical neurons

Figure 8.12 The perceptual process from Chapter 1 (p. 11). Newsome measured relationship C: the physiology–perception relationship, by simultaneously recording from neurons and measuring the monkey's behavioral response. Other research we have discussed has measured relationship A: the stimulus–perception relationship (for example, when flashing two dots creates apparent motion) and relationship B: the stimulus–physiology relationship (for example, when a moving bar causes a cortical neuron to fire).

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connection between how stimuli are moving and neural firing. While all three relationships are important for understanding motion perception, Newsome's demonstration is notable because of the difficulty of simultaneously measuring perception and physiology. This relationship has also been demonstrated (1) by lesioning (destroying) or deactivating some or all of the MT cortex and (2) by electrically stimulating neurons in the MT cortex.

Lesioning the MT Cortex

A monkey with an intact MT cortex can begin detecting the direction dots are moving when coherence is as low as 1 or 2 percent. However, after the MT is lesioned, the coherence must be 10 to 20 percent before monkeys can begin detecting the direction of motion (Newsome & Paré, 1988; also see Movshon & Newsome, 1992; Newsome et al., 1995; Pasternak & Merigan, 1994).

Deactivating the MT Cortex

Further evidence linking neurons in MT cortex to motion perception has been determined from experiments on human participants using a method called **transcranial magnetic stimulation (TMS)** that temporarily disrupts the normal functioning of neurons.

METHOD | Transcranial Magnetic Stimulation (TMS)

One way to investigate whether an area of the brain is involved in determining a particular function is to remove that part of the brain, as noted above for the MT cortex in monkeys. It is possible to temporarily disrupt the functioning of a particular area in humans by applying a strong magnetic field using a stimulating coil placed over the person's skull (**Figure 8.13**).

Figure 8.13 TMS coil positioned to present a magnetic field to the back of a person's head.

A series of electromagnetic pulses presented to a particular area of the brain for a few seconds interferes with brain functioning in that area for seconds or minutes. If a particular behavior is disrupted by the pulses, researchers conclude that the disrupted area of the brain is involved in that behavior.

When researchers applied TMS to the MT cortex, participants had difficulty determining the direction in which a random pattern of dots was moving (Beckers & Homberg, 1992). Although the effect was temporary, these participants experienced a form of akinetopsia much like patient L.M., discussed earlier in this chapter.

Stimulating the MT Cortex

The link between the MT cortex and motion perception has been studied not only by disrupting normal neural activity, but also by enhancing it using a technique called *microstimulation*.

METHOD | Microstimulation

Microstimulation is achieved by lowering a small wire electrode into the cortex and passing a weak electrical charge through the tip of the electrode. This weak shock stimulates neurons that are near the electrode tip and causes them to fire, just as they would if they were being stimulated by chemical neurotransmitters released from other neurons. Thus, after locating neurons that normally respond to certain stimuli using methods such as single-cell recording (p. 22), microstimulation techniques can be used to stimulate those neurons even when these stimuli are absent from the animal's field of view.

Kenneth Britten and coworkers (1992) used this procedure in an experiment in which a monkey was looking at dots moving in a particular direction while indicating the direction of motion it was perceiving. For example, **Figure 8.14a** shows that, under normal conditions, as a monkey observed dots moving to the right, it reported that the dots were indeed moving to the right. **Figure 8.14b**, however, shows how the monkey responded when the researchers stimulated neurons that are activated by downward motion. Instead of perceiving rightward motion, the monkey began responding as though the dots were moving downward and to the right. The fact that stimulating the MT neurons shifted the monkey's perception of the direction of movement provides more evidence linking MT neurons and motion perception.

In addition to the MT cortex, another area highly involved in motion perception is the nearby medial superior temporal (MST) area. The MST area is involved in eye movements, so it is particularly important in localizing a moving object in space. For example, a monkey's ability to reach for a moving object is adversely affected by both microstimulation and lesioning of the MST cortex (Ilg, 2008).

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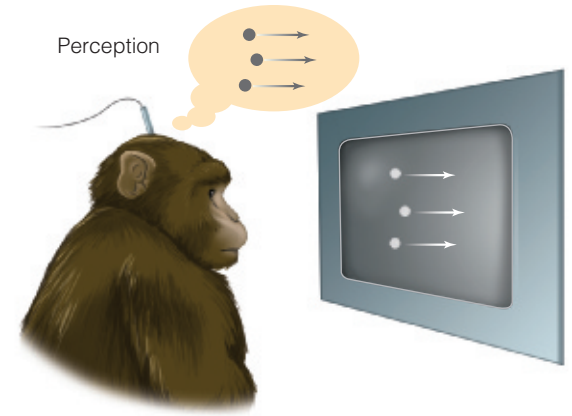
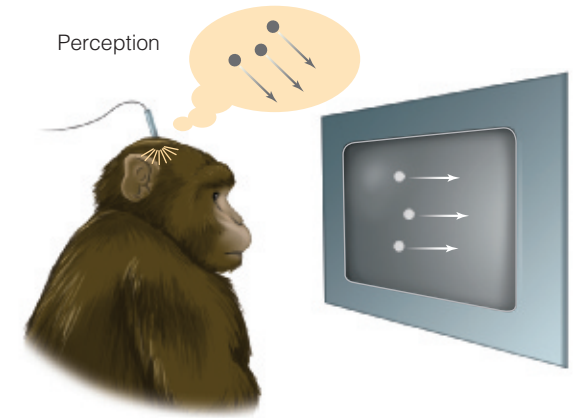


(a) No stimulation



(b) Stimulation

Figure 8.14 (a) A monkey judges the motion of dots moving horizontally to the right. (b) When a column of neurons that are activated by downward motion is stimulated, the monkey judges the same motion as being downward and to the right.

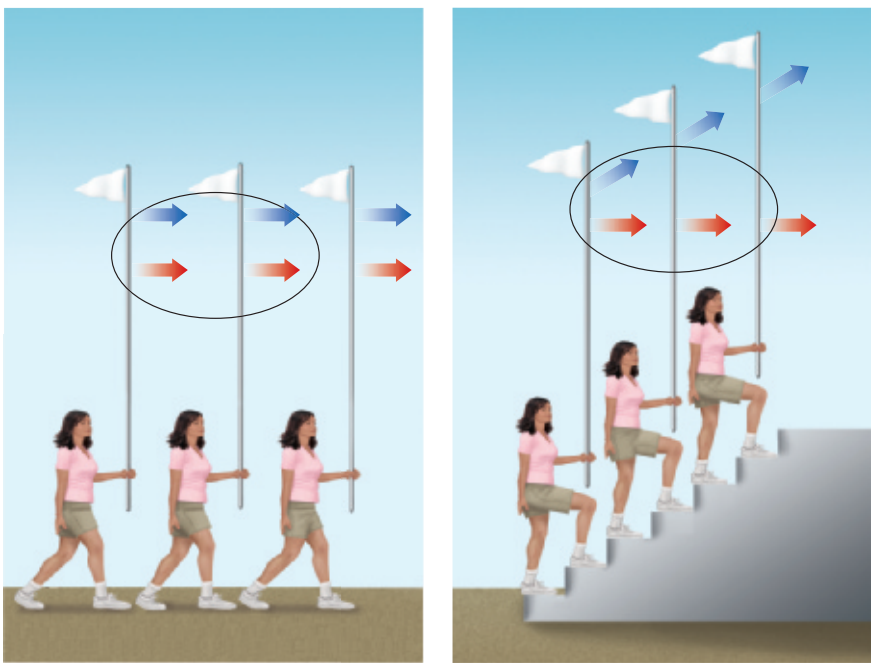
8.7 Beyond Single-Neuron Responses to Motion

We've described a number of research studies which looked at how single neurons fire to movement. As important as these studies are, just showing that a particular neuron responds to motion does not explain how we perceive motion in real life. We can appreciate why this is so by considering how motion signaled by single neurons is ambiguous and can differ from what we perceive (Park & Tadin, 2018). Consider, for example, how a directionally selective neuron would respond to movement of a vertically oriented pole like the one being carried by the woman in **Figure 8.15a**.

We are going to focus on the pole, which is essentially a vertical bar. The ellipse represents the area of the receptive field of a neuron in the cortex that responds when a vertical bar moves to the right across the neuron's receptive field. Figure 8.15a shows the pole entering the receptive field on the left. As the pole moves to the right, it moves across the receptive field in the direction indicated by the red arrow, and the neuron fires.

But what happens if the woman climbs some steps? **Figure 8.15b** shows that as she walks up the steps, she and the pole are now moving up and to the right (blue arrows). We know this because we can see the woman and the flag moving up. But the neuron, which only sees movement through the narrow view of its receptive field, only receives information about the rightward movement (red arrows). This is called the aperture problem, because the neuron's receptive field is functioning like an aperture, which reveals only a small portion of the scene.

Figure 8.15 The aperture problem. (a) The pole's overall motion is horizontally to the right (blue arrows). The ellipse represents the area in an observer's field of view that corresponds to the receptive field of a cortical neuron on the observer's retina. The pole's motion across the receptive field is also horizontal to the right (red arrows). (b) When the woman walks up the steps, the pole's overall motion is up and to the right (blue arrows). However, the pole's motion across the receptive field is horizontal to the right (red arrows), as in (a). Thus, the receptive field "sees" the same motion for motion that is horizontal and motion that is up and to the right.



(a) (b)

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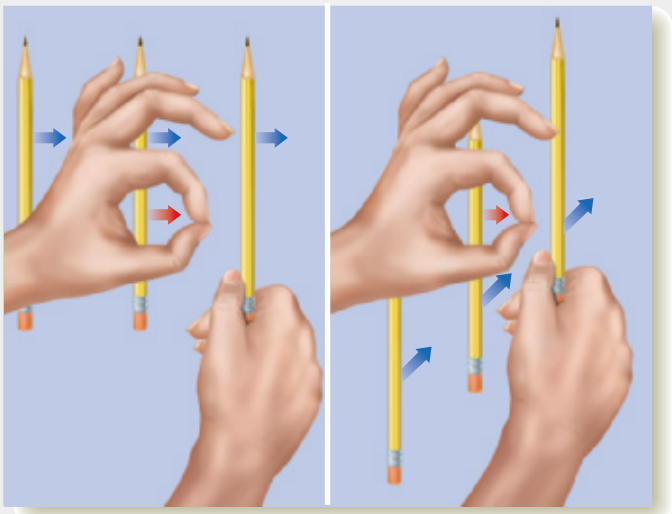
The Aperture Problem

Do the following demonstration to see why the neuron only receives information about rightward movement of the bar.

DEMONSTRATION | Movement of a Bar Across an Aperture

Make a small aperture, about 1 inch in diameter, by creating a circle with the fingers of your left hand, as shown in **Figure 8.16** (or you can create a circle by cutting a hole in a piece of paper). Then orient a pencil vertically, and move the pencil from left to right behind the circle, as shown by the blue arrows in **Figure 8.16a**. As you do this, focus on the direction that the *front edge* of the pencil appears to be moving across the aperture. Now, again holding the pencil vertically, position the pencil below the circle, as shown in **Figure 8.16b**, and move it up behind the aperture at a 45-degree angle (being careful to keep its orientation vertical). Again, notice the direction in which the *front edge* of the pencil appears to be moving across the aperture.



(a) (b)

Figure 8.16 Moving a pencil behind an aperture in the "Movement of a Bar Across an Aperture" demonstration.

If you were able to focus only on what was happening inside the aperture, you probably noticed that the direction that the front edge of the pencil was moving appeared the same whether the pencil was moving (a) horizontally to the right or (b) up and to the right. In both cases, the front edge of the pencil moves across the aperture horizontally, as indicated by the red arrow. Another way to state this is that the movement of an edge across an aperture occurs *perpendicular to the direction in which the edge is oriented*. Because the pencil in our demonstration was oriented vertically, motion through the aperture was horizontal.

Because the motion of the edge was the same in both situations, a single directionally selective neuron would fire similarly in (a) and (b), so based just on the activity of this neuron, it isn't possible to tell whether the pencil is moving horizontally to the right or upward at an angle.

Solutions to the Aperture Problem

There are at least two solutions to the aperture problem (Bruno & Bertamini, 2015). The first was highlighted by one of my students who tried the pencil demonstration in Figure 8.16. He noticed that when he followed the directions for the demonstration, the edge of the pencil did appear to be moving horizontally across the aperture, whether the pencil was moving horizontally or up at an angle. However, he noted that when he moved the pencil so that he could see its tip moving through the aperture, as in **Figure 8.17**, he could tell that the pencil was moving up. Thus, a neuron could use information about the end of a moving object (such as the tip of the pencil) to determine its direction of motion. As it turns out, neurons that could signal this information, because they respond to the ends of moving objects, have been found in the striate cortex (Pack et al., 2003).

The second solution is to pool, or combine, responses from a number of neurons. Evidence for pooling comes from studies in which the activity of neurons in the monkey's MT cortex is recorded while the monkey looks at moving oriented lines like the pole or our pencil. For example, Christopher Pack and Richard Born (2001) found that the MT neurons' initial response to the stimulus, about 70 msec after the stimulus was presented, was determined by the orientation of the bar. Thus the neurons responded in the same way to a vertical bar moving horizontally to the right and a vertical bar moving up and to the right (red arrows in Figure 8.15). However, 140 msec after presentation of the moving bars, the neurons began responding to the *actual* direction in which the bars were moving (blue arrows in Figure 8.15). Apparently, MT neurons receive signals from a number of neurons in the striate cortex and then combine these signals to determine the actual direction of motion.

What all of this means is that the "simple" situation of an object moving across the visual field as an observer looks

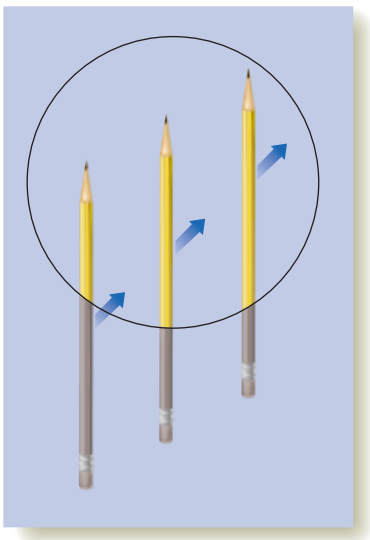


Figure 8.17 The circle represents a neuron's receptive field. When the pencil is moved up and to the right, as shown, movement of the tip of the pencil provides information indicating that the pencil is moving up and to the right.

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straight ahead is not so simple because of the aperture problem. The visual system apparently solves this problem (1) by using information from neurons in the striate cortex that respond to the movement of the ends of objects and (2) by using information from neurons in the MT cortex that pool the responses of a number of directionally selective neurons (also see Rust et al., 2006; Smith et al., 2005; Zhang & Britten, 2006).

8.8 Motion and the Human Body

Experiments using dots and lines as stimuli have taught us a great deal about the mechanisms of motion perception, but what about the more complex stimuli created by moving humans and animals that are so prevalent in our environment? We will now consider two examples of the ways in which researchers have studied how we perceive movement of the human body.

Apparent Motion of the Body

Earlier in this chapter we described *apparent motion* as the perception of motion that occurs when two stimuli that are in slightly different locations are presented one after the other. Even though these stimuli are stationary, movement is perceived back and forth between them if they are alternated with the correct timing. Generally, this movement follows a principle called the **shortest path constraint**—apparent movement tends to occur along the shortest path between two stimuli.

Maggie Shiffrar and Jennifer Freyd (1990, 1993) had observers view photographs like the ones in **Figure 8.18a**, with the photographs alternating rapidly. Notice that in the first picture, the woman's hand is in front of her head, and in the second, it is behind her head. According to the shortest path constraint, motion should be perceived in a straight line between the hands in the alternating photos, which means observers would see the woman's hand as moving through her head, as shown in **Figure 8.18b**. This is, in fact, exactly what happens when the pictures are alternated very rapidly (five or more times a second), even though motion through the head is physically impossible.

While the straight-line motion of the hand through the head is an interesting result, the most important result occurred when the rate of alternation was slowed. When the pictures were alternated less than five times per second, observers began perceiving the motion shown in **Figure 8.18c**: the hand appeared to move around the woman's head. These results are interesting for two reasons: (1) They show that the visual system needs time to process information in order to perceive the movement of complex meaningful stimuli. (2) They suggest that there may be something special about the meaning of the stimulus—in this case, the human body—that influences the way movement is perceived. To test the idea that the human body is special, Shiffrar and coworkers showed that when objects such as boards are used as stimuli, the likelihood of perceiving movement along the longer path does not increase at lower rates of alternation, as it does for pictures of humans (Chatterjee et al., 1996).

What is happening in the cortex when observers view apparent motion generated by pictures like the ones in Figure 8.18? To find out, Jennifer Stevens and coworkers (2000) measured brain activation using brain imaging. They found that both movement through the head and movement around the head activated areas in the parietal cortex associated with movement. However, when the observers saw movement as occurring around the head, the motor cortex was activated as well. Thus, the motor cortex is activated when the perceived movements are humanly possible but isn't activated when the perceived movements are not possible. This connection between the brain area associated with perceiving movement and the motor area reflects the close connection between perception and taking action that we discussed in Chapter 7.

Biological Motion Studied by Point-Light Walkers

An approach to studying motion of the human body that we introduced at the beginning of the chapter involves *point-light walkers*, which are created by placing small lights on people's

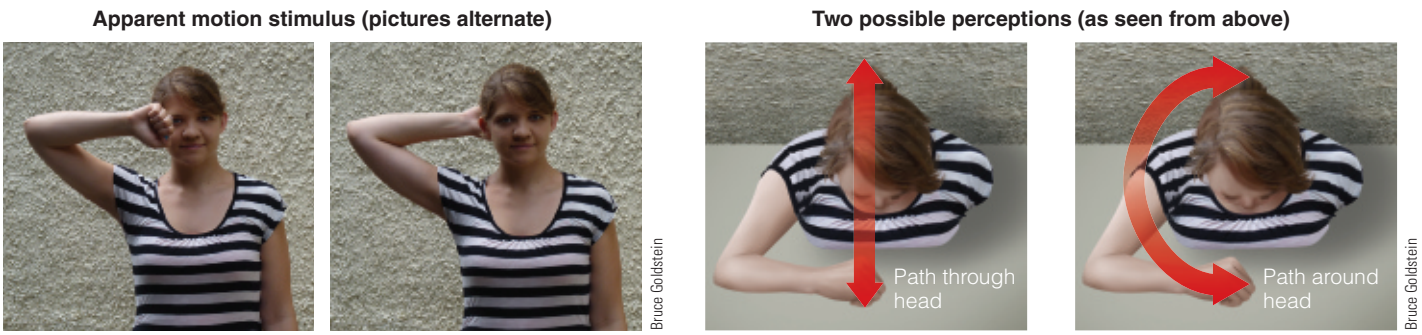

Figure 8.18 The two pictures in (a) are photographs similar to those used in Shiffrar and Freyd's (1993) experiment. The pictures were alternated either rapidly or more slowly. (b) When alternated rapidly, observers perceived the hand as moving through the head. (c) When alternated more slowly, the hand was seen as moving around the head.

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joints and then filming the patterns created by these lights when people move (see Figure 8.4).

Research using point-light walkers shows that motion of the body creates perceptual organization by causing the movements of the individual dots to become organized into "a person moving." When the person wearing the lights is stationary, the lights look like a meaningless pattern. However, as soon as the person starts walking, with arms and legs swinging back and forth and feet moving in flattened arcs, first one leaving the ground and touching down, and then the other, the motion of the lights is immediately perceived as being caused by a walking person. This self-produced motion of a person or other living organism is called **biological motion**.

One reason we are particularly good at perceptually organizing the complex motion of an array of moving dots into the perception of a walking person is that we see biological motion all the time. Every time you see a person walking, running, or behaving in any way that involves movement, you are seeing biological motion.

Our ability to easily perceive biological motion in moving points of light led some researchers to suspect that there may be a specific area in the brain that responds to biological motion, just as there are areas such as the extrastriate body area (EBA) and fusiform face area (FFA) that are specialized to respond to bodies and faces, respectively (see page 111 and Figures 5.41, 5.42, and 5.43).

Emily Grossman and Randolph Blake (2001) provided evidence supporting the idea of a specialized area in the brain for biological motion by measuring observers' brain activity as they viewed the moving dots created by a point-light walker (**Figure 8.19a**) and as they viewed dots that moved similarly to the point-light walker dots, but were scrambled so they did not result in the impression of a person walking (**Figure 8.19b**). They found that a small area in the superior temporal sulcus (STS) (see Figure 5.42) was more active when viewing biological motion than viewing scrambled motion in all eight of their observers.

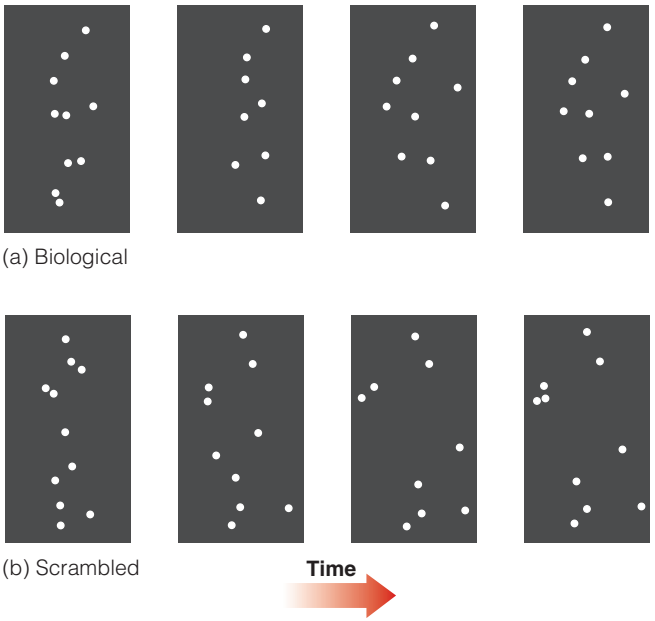
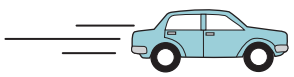


Figure 8.19 Frames from the stimuli used by Grossman and Blake (2001). (a) Sequence from the point-light walker stimulus. (b) Sequence from the scrambled point-light stimulus.

In later experiments, researchers determined that other brain areas are also involved in the perception of biological motion. For example, both the FFA (Grossman & Blake, 2002) and the portions of the PFC that contain mirror neurons (see Figure 7.18) (Saygin et al., 2004) are activated more by biological motion than by scrambled motion. Based on these results, researchers have concluded that there is a network of areas that together are specialized for the perception of biological motion (also see Grosbras et al., 2012; Grossman et al., 2000; Pelphrey et al., 2003, 2005; Saygin, 2007, 2012). See **Table 8.1** for a summary of the structures involved in motion perception that we have discussed in this chapter.

Table 8.1 Brain Regions Involved in the Perception of Motion

BRAIN REGION	FUNCTIONS RELATED TO MOTION	EXAMPLE
Striate Cortex (V1)	Direction of motion across small receptive fields	
Middle Temporal (MT) Area	Direction and speed of object motion	
Medial Superior Temporal (MST) Area	Processing optic flow; locating moving objects; reaching for moving objects	
Superior Temporal Sulcus (STS)	Perception of motion related to animals and people (biological motion)	

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Earlier in the chapter we described how Newsome used a number of different methods to show that the MT cortex is specialized for the perception of motion (p. 18). In addition to showing that the MT cortex is *activated* by motion, he also showed that *perception* of motion is decreased by lesioning the MT cortex and is influenced by stimulating neurons in the MT cortex. Just as Newsome showed that disrupting operation of the MT cortex decreases a monkey's ability to perceive the direction of moving dots, Emily Grossman and coworkers (2005) showed that using transcranial magnetic stimulation (TMS) to disrupt the operation of the STS in humans decreases the ability to perceive biological motion (see "Method: Transcranial Magnetic Stimulation," page 185).

The observers in Grossman's (2005) experiment viewed point-light stimuli for activities such as walking, kicking, and throwing (**Figure 8.20a**), and they also viewed scrambled point-light displays (**Figure 8.20b**). Their task was to determine whether a display was biological motion or scrambled motion. This is normally an extremely easy task, but Grossman made it more difficult by adding extra dots to create "noise" (**Figures 8.20c** and **8.20d**). The amount of noise was adjusted for each observer so that they could distinguish between biological and scrambled motion with 71 percent accuracy.

The key result of this experiment was that presenting transcranial magnetic stimulation to the area of the STS that is activated by biological motion caused a significant decrease in the observers' ability to perceive biological motion. Such magnetic stimulation of other motion-sensitive areas, such as the MT cortex, had no effect on the perception of biological motion. From this result, Grossman concluded that normal functioning of the "biological motion" area, STS, is necessary for perceiving biological motion. This conclusion is also supported by studies showing that people who have suffered damage to this area have trouble perceiving biological motion (Battelli et al., 2003). The ability to discriminate biological motion from randomly moving dots has also been shown to be adversely affected when transcranial magnetic stimulation is applied to other regions involved in the perception of biological motion, such as the prefrontal cortex (PFC, see Figure 7.18) (van Kemenade et al., 2012). What all of this means is that biological motion is more than just "motion"; it is a special type of motion that is served by specialized areas of the brain.

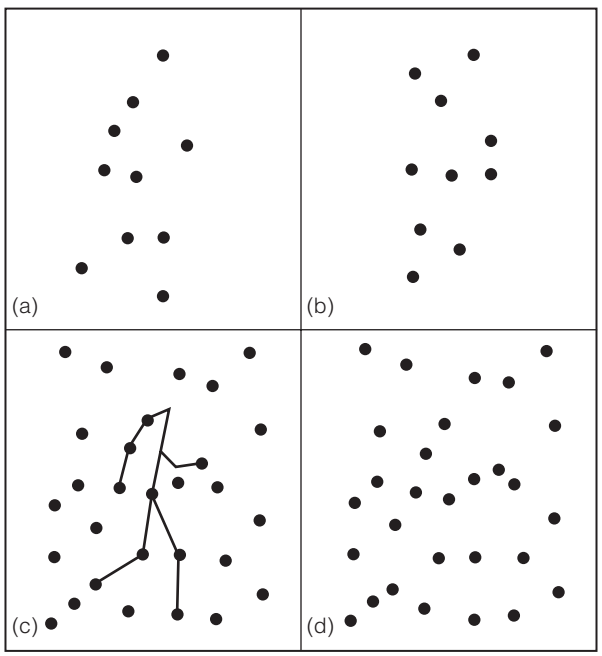

Figure 8.20 (a) Biological motion stimulus. (b) Scrambled stimulus. (c) Biological motion stimulus with noise added. The dots corresponding to the walker are indicated by lines (which were not seen by the observer). (d) How the stimulus appeared to the observer. (From Grossman et al., 2005)

8.9 Motion Responses to Still Pictures

Consider the picture in **Figure 8.21**, which most people perceive as a "freeze frame" of an action—skiing—that involves motion. It is not hard to imagine the person moving to a different location immediately after this picture was taken. A situation such as this, in which a still picture depicts an action involving motion, is called **implied motion**. Despite the lack of either real motion or apparent motion in this situation, a variety of experiments have shown that the perception of implied motion depends on many of the mechanisms we have introduced in this chapter.

Jennifer Freyd (1983) conducted an experiment involving implied motion by briefly showing observers pictures that depicted a situation involving motion, such as a person jumping off a low wall (**Figure 8.22a**). Freyd predicted that participants looking at this picture would "unfreeze" the implied motion depicted in the picture and anticipate the motion that was about to happen. If this occurred, observers might "remember" the picture as depicting a situation that occurred slightly later in time. For the picture of the person jumping off the wall, that would mean the observers might remember the person as being closer to the ground (as in **Figure 8.22b**) than he was in the initial picture.

Ales Fevzer/Encyclopedia/Corbis

Figure 8.21 A picture that creates implied motion.

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(a) First picture (b) Forward in time (c) Backward in time

Figure 8.22 Stimuli like those used by Freyd (1983). See text for details.

To test this idea, Freyd showed participants a picture of a person in midair, like Figure 8.22a, and then after a pause, she showed her observers either (1) the same picture; (2) a picture slightly forward in time (the person who had jumped off the wall was closer to the ground, as in Figure 8.27b); or (3) a picture slightly backward in time (the person was farther from the ground, as in **Figure 8.22c**). The observers' task was to indicate, as quickly as possible, whether the second picture was the same as or different from the first picture.

When Freyd compared the time it took for participants to decide if the "time-forward" and "time-backward" pictures were different from the first picture they had seen, she found that participants took longer to decide if the time-forward picture was the same or different. She concluded from this that the time-forward judgment was more difficult because her participants had anticipated the downward motion that was about to happen and so confused the time-forward picture with what they had actually seen.

The idea that the motion depicted in a picture tends to continue in the observer's mind is called **representational momentum** (David & Senior, 2000; Freyd, 1983). Representational momentum is an example of experience influencing perception because it depends on our knowledge of the way situations involving motion typically unfold.

If implied motion causes an object to continue moving in a person's mind, then it would seem reasonable that this continued motion might be reflected by activity in the brain. When Zoe Kourtzi and Nancy Kanwisher (2000) measured the fMRI response in the MT and MST cortex to pictures like the ones in **Figure 8.23**, they found that the area of the brain that responds to actual motion also responds to *pictures* of motion, and that implied-motion (IM) pictures caused a greater response than no-implied-motion (no-IM) pictures, at rest (R) pictures, or house (H) pictures. Thus, activity occurs in the brain that corresponds to the continued motion that implied-motion pictures create in a person's mind (also see Lorteije et al., 2006; Senior et al., 2000).

Building on the idea that the brain responds to implied motion, Jonathan Winawer and coworkers (2008) wondered whether still pictures that implied motion, like the one in Figure 8.21, would elicit a motion aftereffect (see page 179). To test this, they conducted a psychophysical experiment in which they asked whether viewing still pictures showing implied motion in a particular direction can cause a motion aftereffect in the opposite direction. We described one type of motion aftereffect at the beginning of the chapter by noting that after viewing the downward movement of a waterfall, nearby stationary objects appear to move upward. There is

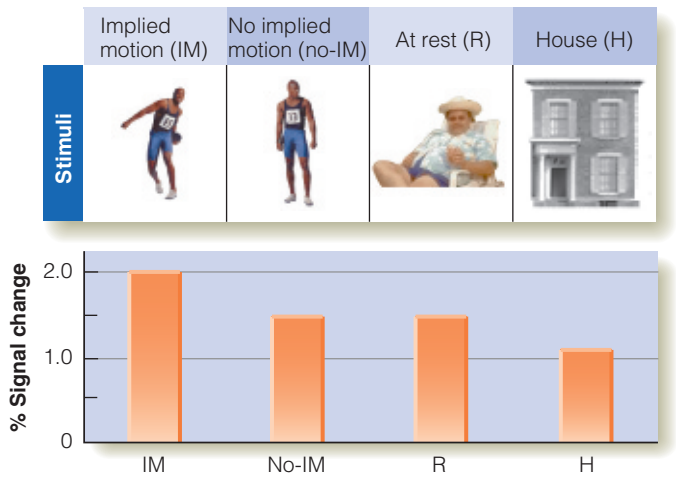

Figure 8.23 Examples of pictures used by Kourtzi and Kanwisher (2000) to depict implied motion (IM), no implied motion (no-IM), "at rest" (R), and a house (H). The height of the bar below each picture indicates the average fMRI response of the MT cortex to that type of picture. (From Kourtzi & Kanwisher, 2000)

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evidence that this occurs because prolonged viewing of the waterfall's downward motion decreases the activity of neurons that respond to downward motion, so more upward motion neuronal activity remains (Barlow & Hill, 1963; Mather et al., 1998).

To determine whether implied motion stimuli would have the same effect, Winawer had his participants observe a series of pictures showing implied motion. For a particular trial, participants saw either a series of pictures that all showed movement to the right or a series of pictures that all showed movement to the left. After adapting to this series of pictures for 60 seconds, the participants' task was to indicate the direction of movement of arrays of moving dots like the ones we described earlier (see Figure 8.11).

The key result of this experiment was that before observing the implied-motion stimuli, participants were equally likely to perceive dot stimuli with zero coherence (all the dots moving in random directions) as moving to the left or to the right. However, after viewing photographs showing rightward implied motion, participants were more likely to see the dots as moving to the left. After viewing leftward implied motion, participants were more likely to see the randomly moving dots as moving to the right. Because this is the same result that would occur for adapting to real movement to the left or right, Winawer concluded that viewing implied motion in pictures decreases the activity of neurons selective to that direction of motion.

SOMETHING TO CONSIDER:

Motion, Motion, and More Motion

There's a well-known question about real estate that asks, "What are the three things that determine the value of a house?" The answer: Location, location, and location. Although our topic is far from real estate, we can, looking back on the last three chapters, ask a question with a similar three-part answer: "What kept happening, throughout Chapters 6, 7, and 8?" The answer: Motion, motion, and then more motion.

Chapter 6, "Visual Attention," isn't all about motion, but there was a lot of movement, nonetheless, because the eyes are in constant motion as we scan a scene, and movement is one of the main aspects of the environment that attracts attention. Chapter 7, "Taking Action," was about all kinds of movement: walking, driving, moving through the environment, reaching, grasping, watching other people move, and considering how infants move. Chapter 7, it is accurate to say, is about movement of the body. And finally, this chapter offered a change of perspective, as we shifted from *doing movement* to *perceiving movement* and taking advantage of its many functions.

There's an important message here. Movement, in all its forms, is essential for survival. It helps us know where we are, avoid potential dangers, act in many different ways in and on the environment, and gain access to a wealth of information about the environment. Because movement is so important, it is not surprising that it took three chapters to describe it, and although we will be taking a short break from movement as we discuss color vision in Chapter 9, we will encounter movement again in Chapter 10, as we show how movement helps us perceive depth, in Chapter 12, as we consider how we perceive moving sounds, and in Chapter 15, as we consider how we perceive motion across our skin. Motion, as it turns out, is one of the central phenomena in our lives and, therefore, in perception as well.

DEVELOPMENTAL DIMENSION Infants Perceive Biological Motion

Many accounts of biological motion perception argue that our own experiences with people and animals are critical for developing the ability to perceive biological motion. Evidence for this claim comes, in part, from developmental studies that have shown that a child's ability to recognize biological motion in point-light displays improves as he or she gets older (Freire et al., 2006; Hadad et al., 2011). In fact, some studies suggest that adultlike levels of performance on point-light tasks are not achieved until early adolescence (Hadad et al., 2011). But even though it may take years to reach adult levels of performance, some research suggests that the ability to distinguish biological from nonbiological motion may be present at birth.

One line of evidence suggesting that the perception of biological motion may not depend on visual experience comes from animal studies. For example, Giorgio

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Vallortigara and his coworkers (2005) found that if newborn chicks with no prior visual experience are presented with two movement displays (1) the "walking hen," point light display which shows dots that would be created by a moving hen and (2) the same number of dots moving randomly (**Figure 8.24a**). When these displays were shown at opposite ends of a platform (**Figure 8.24b**) the chicks spent most of their time near the biological movement display. This indicates that the chicks were able to identify—and, in fact, preferred—the biological motion displays despite not having had any prior visual experience. In order for this to happen, Vallortigara argued, chicks must possess perceptual mechanisms tuned to biological motion prior to hatching.

Intrigued by Vallortigara's experiments with newly hatched chicks, Francesca Simion and her coworkers (2008) wondered whether similar biological motion detector mechanisms might also be present in newborn humans. To find out, the researchers conducted a version of the chick study with 1- and 2-day-old newborns using the preferential looking procedure (see Chapter 3, page 60).

Simion conducted her experiment in the maternity ward of a hospital with full-term newborns. Infants in the study sat on an adult's lap while they were shown two movies simultaneously on side-by-side computer monitors (**Figure 8.24c**). On one screen, infants saw 14 point-lights moving in random directions. On the other screen, they were shown a movie where the 14 moving point-lights depicted the same walking hen used by Vallortigara in his experiment with chicks. Simion used the hen-walking animation because she could not ethically deprive the newborns of any visual experience prior to their participation in her study. So, the newborns may have obtained some *very* limited experience with human motion prior to the experiment, but it was very unlikely that they had seen any hens wandering about the hospital.

The researchers wanted to know if these newborns, like newly hatched chicks, would prefer the biological motion display to the random point-light display. They therefore compared the amount of time the infants spent looking at each movie. They discovered that the infants spent 58 percent of their time looking at the point-light hen, which was statistically greater than the time spent looking at the random point-light display. Thus, Simion and her colleagues concluded that, like chicks, humans are born with an ability to detect biological motion.

From their results, both Vallortigara and Simion argued that the ability to perceive biological motion occurs independent of experience. However, there is also evidence that the perception of biological motion changes with age.

It would be logical to assume that if newborns are sensitive to biological motion, this ability would then improve as they experience more biological motion. However, research on older infants shows that response to biological motion decreases to zero at 1 or 2 months of age, and then returns by 3 months and increases over the next two years of life and beyond (Sifre et al., 2018).

What's going on? One idea is that two different mechanisms are involved. At birth a reflex-like mechanism is sensitive to biological motion. This is useful to the newborn because it helps them react to caregivers. By 2 months this mechanism no longer functions, but a second mechanism begins emerging at around 3 months. An important property of this mechanism is that its performance improves as infants accumulate more experience observing biological motion. This helps the infant relate to caregivers on a more complex level as they transition from stationary observers of people moving relative to them, to active observers, whose crawling and walking help them develop social skills as they interact with other biologically-moving beings (see Developmental Dimension: Infant Affordances, Chapter 7, page 169).

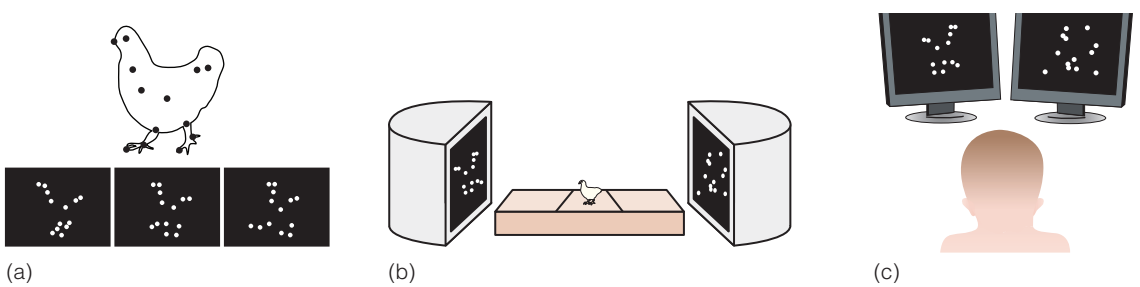

Figure 8.24 (a) Top: placement of point-lights on an adult hen. Bottom: still images from an animated movie depicting a walking hen and also random dots. (b) The testing apparatus used by Vallortigara et al. (2005) to measure chicks' reactions to biological motion stimuli. Stimuli were shown on the monitors at each end of a platform. A chick's preference for one stimulus over the other is revealed by the amount of time the chick spends at each end of the platform. (c) The testing apparatus used by Simion et al. (2008) to measure newborn reactions to biological motion. The newborn's preference for one stimulus over the other was revealed by the amount of time the newborn spent looking at each stimulus.

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TEST YOURSELF 8.2

1. Describe the operation of the neural circuit that creates the Reichardt detector. Be sure you understand why the circuit leads to firing to movement in one direction, but no firing to movement in the opposite direction.
2. What is the evidence that the MT cortex is specialized for processing movement? Describe the series of experiments that used moving dots as stimuli and (a) recorded from neurons in the MT cortex, (b) lesioned the MT cortex, and (c) stimulated neurons in the MT cortex. What do the results of these experiments enable us to conclude about the role of the MT cortex in motion perception?
3. Describe the aperture problem—why the response of individual directionally selective neurons does not provide sufficient information to indicate the direction of motion. Also describe two ways that the brain might solve the aperture problem.
4. Describe experiments on apparent motion of a person's arm. How do the results differ for slow and fast presentations of the stimuli? How is the brain activated by slow and fast presentations?
5. What is biological motion, and how has it been studied using point-light displays?
6. Describe the experiments that have shown that an area in the superior temporal sulcus (STS) is specialized for perceiving biological motion.
7. What is implied motion? Representational momentum? Describe behavioral evidence demonstrating representational momentum, physiological experiments that investigated how the brain responds to implied motion stimuli, and the experiment that used photographs to generate a motion aftereffect.
8. Describe how experiments with young animals and infants have been used to determine the origins of biological motion perception. What is the evidence that there may be two mechanisms of early biological motion perception?

THINK ABOUT IT

1. We described the role of the Reichardt detector in the perception of real motion that occurs when we see things that are physically moving, such as cars on the road and people on the sidewalk. Explain how the detector illustrated in Figure 8.10 could also be used to detect the kinds of apparent motion on TV, in movies, on our computer screens, and in electronic displays such as those in Las Vegas or Times Square.
2. In the present chapter we have described a number of principles that also hold for object perception (Chapter 5). Find examples from Chapter 5 of the following (page numbers are for this chapter):
   - There are neurons that are specialized to respond to specific stimuli (p. 183).
   - More complex stimuli are processed in higher areas of the cortex (p. 189).
   - Experience can affect perception (p. 190).
   - There are parallels between physiology and perception (pp. 184, 188, 191).
3. We described how the representational momentum effect shows how knowledge can affect perception. Why could we also say that representational momentum illustrates an interaction between perception and memory?

KEY TERMS

Akinetopsia (p. 175)
Aperture problem (p. 186)
Apparent motion (p. 179)
Biological motion (p. 189)
Coherence (p. 184)
Comparator (p. 181)
Corollary discharge signal (CDS) (p. 181)
Corollary discharge theory (p. 181)
Delay unit (p. 182)
Event (p. 177)
Event boundary (p. 177)
Global optic flow (p. 181)
Illusory motion (p. 179)
Image displacement signal (IDS) (p. 181)
Implied motion (p. 190)
Induced motion (p. 179)
Local disturbance in the optic array (p. 181)
Microstimulation (p. 185)
Middle temporal (MT) area (p. 183)
Motion aftereffect (p. 179)
Motor signal (MS) (p. 181)
Optic array (p. 181)
Output unit (p. 182)
Point-light walker (p. 178)
Real motion (p. 179)
Reichardt detector (p. 182)
Representational momentum (p. 191)
Shortest path constraint (p. 188)
Transcranial magnetic stimulation (TMS) (p. 185)
Waterfall illusion (p. 179)

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What's amazing about this picture is not only that the umbrellas appear to be floating, but that your perception of their colors is created by your nervous system when light that has no color is reflected from the umbrellas into your eyes and activates three types of cone receptors in the retina. How colorless light can cause color will be explained in this chapter.

Bruce Goldstein

Learning Objectives

After studying this chapter, you will be able to …

- Describe a number of important functions of color perception.
- Understand the relationship between the wavelength of light and color and be able to apply this to explaining what happens when wavelengths are mixed.
- Understand how we can perceive millions of colors even though there are only six or seven colors in the visible spectrum.
- Describe the trichromatic theory of color vision and how the theory explains color deficiency.
- Describe the opponent-process theory of color vision, and why some researchers have questioned a proposed link between opponent neural responding and color perception.
- Understand limitations on our understanding of how color is represented in the cortex.
- Describe experiments that show that we need to go beyond wavelength in order to fully understand color perception.
- Understand what it means to say that we perceive color from colorless wavelengths.
- Describe how behavioral experiments have been used to study infant color vision.

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CHAPTER 9

Perceiving Color

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DEVELOPMENTAL DIMENSION: Infant Color Vision

TEST YOURSELF 9.4

THINK ABOUT IT

Some Questions We Will Consider:

- Why does mixing yellow and blue paints create green? (p. 201)
- Why do colors look the same indoors and outdoors? (p. 215)
- Does everyone perceive color the same way? (pp. 207, 218, 224)

Color is one of the most obvious and pervasive qualities in our environment. We interact with it every time we note the color of a traffic light, choose clothes that are color coordinated, or appreciate the colors of a painting. We pick favorite colors (blue is the most favored; Terwogt & Hoeksma, 1994), we associate colors with emotions (we turn purple with rage, red with embarrassment, green with envy, and feel blue; Terwogt & Hoeksma, 1994; Valdez & Mehrabian, 1994), and we imbue colors with special meanings (for example, in many cultures red signifies danger; purple, royalty; green, ecology). But for all of our involvement with color, we sometimes take it for granted, and—just as with our other perceptual abilities—we may not fully appreciate color unless we lose our ability to experience it. The depth of this loss is illustrated by the case of Mr. I., a painter who became color blind at the age of 65 after suffering a concussion in an automobile accident.

In March 1986, the neurologist Oliver Sacks received a letter from Mr. I., who, identifying himself as a "rather successful artist," described how, ever since he had been involved in an automobile accident, he had lost his ability to experience colors. He exclaimed with some anguish, "My dog is gray. Tomato juice is black. Color TV is a hodge-podge. ..." In the days following his accident, Mr. I. became more and more depressed. His studio, normally awash with the brilliant colors of his abstract paintings, appeared drab to him, and his paintings, meaningless. Food, now gray, became difficult for him to look at while eating, and sunsets, once seen as rays of red, had become streaks of black against the sky (Sacks, 1995).

Mr. I.'s color blindness, a condition called **cerebral achromatopsia**, was caused by cortical injury after a lifetime of experiencing color, whereas most cases of total color

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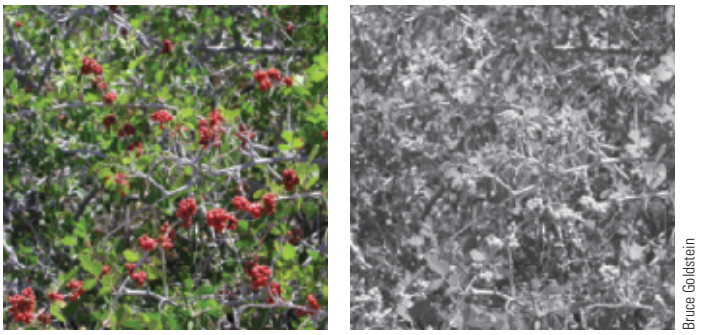
blindness or of **color deficiency** (partial color blindness, which we'll discuss in more detail later in this chapter) occur at birth because of the genetic absence of one or more types of cone receptors. Most people who are born partially color blind are not disturbed by their decreased color perception compared to "normal," because they have never experienced color as a person with normal color vision does. However, some of their reports, such as the darkening of reds, are similar to Mr. I.'s. People with total color blindness often echo Mr. I.'s complaint that it is sometimes difficult to distinguish one object from another, as when his brown dog, which he could easily see silhouetted against a light-colored road, became very difficult to perceive when seen against irregular foliage.

Eventually, Mr. I. overcame his strong psychological reaction and began creating striking black-and-white pictures. But his account of his color-blind experiences provides an impressive testament to the central place of color in our everyday lives. (See Heywood et al., 1991; Nordby, 1990; Young et al., 1980; and Zeki, 1990, for additional descriptions of cases of complete color blindness.) Besides adding beauty to our lives, color has other functions as well.



(a) (b)

Figure 9.1 (a) Red berries in green foliage. (b) These berries become more difficult to detect without color vision.

(a) (b)

Figure 9.2 Participants in Tanaka and Presnell's (1999) experiment were able to recognize appropriately colored objects like the fruits in (a) more rapidly than inappropriately colored objects like the fruits in (b).

9.1 Functions of Color Perception

Color serves important signaling functions, both natural and contrived by humans. The natural and human-made world provides many color signals that help us identify and classify things: we know a banana is ripe when it has turned yellow, and we know to stop when the traffic light turns red.

In addition to its signaling function, color helps facilitate perceptual organization (Smithson, 2015), the processes discussed in Chapter 5 by which similar elements become grouped together and objects are segregated from their backgrounds (see Figures 5.18 and 5.19 on pages 97–98).

Color's role in perceptual organization is crucial to the survival of many species. Consider, for example, a monkey foraging for fruit in the forest or jungle. A monkey with good color vision easily detects red fruit against a green background (**Figure 9.1a**), but a color-blind monkey would find it more difficult to find the fruit (**Figure 9.1b**). Color vision thus enhances the contrast of objects that, if they didn't appear colored, would be more difficult to perceive.

This link between good color vision and the ability to detect colored food has led to the proposal that monkey and human color vision may have evolved for the express purpose of detecting fruit (Mollon, 1989, 1997; Sumner & Mollon, 2000; Walls, 1942). This suggestion sounds reasonable when we consider the difficulty that color-blind humans have when confronted with the seemingly simple task of picking berries. Knut Nordby (1990), a totally color-blind vision scientist who sees the world in shades of gray, has described his own experience: "Picking berries has always been a big problem. I often have to grope around among the leaves with my fingers, feeling for the berries by their shape" (p. 308).

Our ability to perceive color not only helps us detect objects that might otherwise be obscured by their surroundings, it also helps us recognize and identify things we can see easily. James Tanaka and Lynn Presnell (1999) demonstrated this by asking observers to identify objects like the ones in **Figure 9.2**, which appeared either in their normal colors, like the yellow banana, or in inappropriate colors, like the purple banana. The result was that observers recognized the appropriately colored objects more rapidly and accurately. Thus, knowing the colors of familiar objects helps us to recognize these objects (Oliva & Schyns, 2000; Tanaka et al., 2001). Expanding our view beyond single objects, color also helps us recognize natural scenes (Gegenfurtner & Rieger, 2000) and rapidly perceive the gist of scenes (Castelhano & Henderson, 2008) (see Figure 5.33, page 105).

It has also been suggested that color can be a cue to emotions signaled by facial expressions. This was demonstrated by Christopher Thorstenson and coworkers (2019) who found that when asked to rate the emotions of ambiguous-emotion faces like the one in **Figure 9.3**, participants were more likely to rate the face as expressing disgust when colored green and as expressing anger when red.

In the discussion that follows, we will consider how our nervous system creates our perception of color. We begin by considering the relationship between color and light, and will then consider two theories of color vision.

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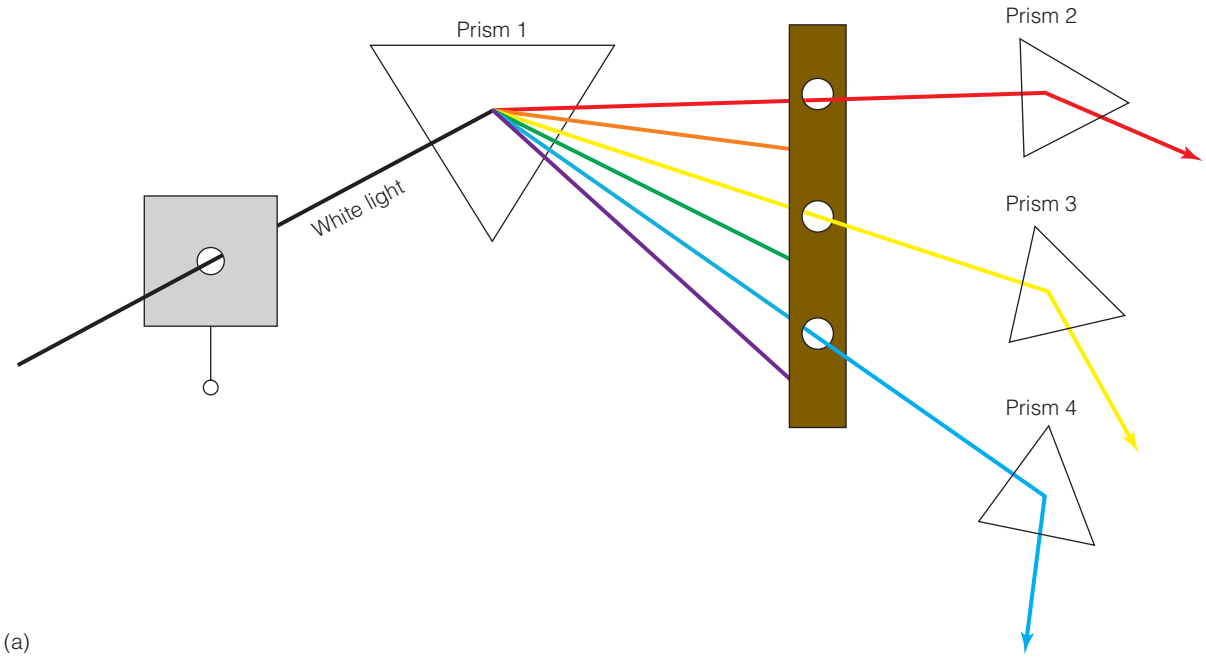
Christopher Baker

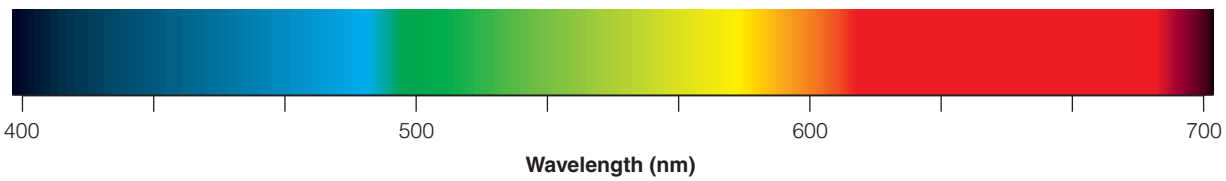
Figure 9.3 How do you perceive the emotion of each of these versions of the same face? Color has been shown to influence emotion judgments, with red associated with "anger" and green associated with "disgust."

9.2 Color and Light

For much of his career, Isaac Newton (1642–1727) studied the properties of light and color. One of his most famous experiments is diagrammed in **Figure 9.4a** (Newton, 1704). First, Newton made a hole in a window shade, which let a beam of sunlight enter the room. When he placed Prism 1 in its path, the beam of white-appearing light was split into the components of the visual spectrum shown in **Figure 9.4b**. Why did this happen? At the time, many people thought that prisms (which were common novelties) *added* color to light. Newton,



(a)



(b)

Figure 9.4 (a) Diagram of Newton's prism experiment. Light entered through a hole in the window shade and then passed through the prism. The colors of the spectrum were then separated by passing them through holes in a board. Each color of the spectrum then passed through a second prism. Different colors were bent by different amounts. (b) The visible spectrum.

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however, thought that white light was a mixture of differently colored lights and that the prism separated the white light into its individual components. To support this hypothesis, Newton next placed a board in the path of the differently colored beams. Holes in the board allowed only particular beams to pass through while the rest were blocked. Each beam that passed through the board then went through a second prism, shown as Prisms 2, 3, and 4, for the red, yellow, and blue rays of light.

Newton noticed two important things about the light that passed through the second prism. First, the second prism did not change the color appearance of any light that passed through it. For example, a red beam continued to look red after it passed through the second prism. To Newton, this meant that unlike white light, the individual colors of the spectrum are not mixtures of other colors. Second, the degree to which beams from each part of the spectrum were "bent" by the second prism was different. Red beams were bent only a little, yellow beams were bent a bit more, and violet beams were bent the most. From this observation, Newton concluded that light in each part of the spectrum is defined by different physical properties and that these physical differences give rise to our perception of different colors.

Throughout his career, Newton was embroiled in debate with other scientists regarding what the physical differences were between differently colored lights. Newton thought that prisms separated differently colored light particles while others thought the prism separated light into differently colored waves. Clarity on these matters would come in the 19th century when scientists conclusively showed that the colors of the spectrum are associated with different wavelengths of light (Figure 9.4b). Wavelengths from about 400 to 450 nm appear violet; 450 to 490 nm, blue; 500 to 575 nm, green; 575 to 590 nm, yellow; 590 to 620 nm, orange; and 620 to 700 nm, red. Thus, our perception of color depends critically on the wavelengths of light that enter our eyes.

Reflectance and Transmission

The colors of *light* in the spectrum are related to their wavelengths, but what about the colors of *objects*? The colors of objects are largely determined by the wavelengths of light that are *reflected* from the objects into our eyes. Chromatic colors, such as blue, green, and red, occur when some wavelengths are reflected more than others, a process called selective reflection. The sheet of paper illustrated in **Figure 9.5a** reflects long wavelengths of light and absorbs short and medium wavelengths. As a result, only the long wavelengths reach our eyes, and the paper appears red. Achromatic colors, such as white, gray, and black, occur when light is reflected equally across the spectrum. Because the sheet of paper in **Figure 9.5b** reflects all wavelengths of light, it appears white.

Individual objects don't usually reflect a single wavelength of light, however. **Figure 9.6a** shows reflectance curves that plot the percentage of light reflected from lettuce and tomatoes at each wavelength in the visible spectrum. Notice that both vegetables reflect a range of wavelengths, but

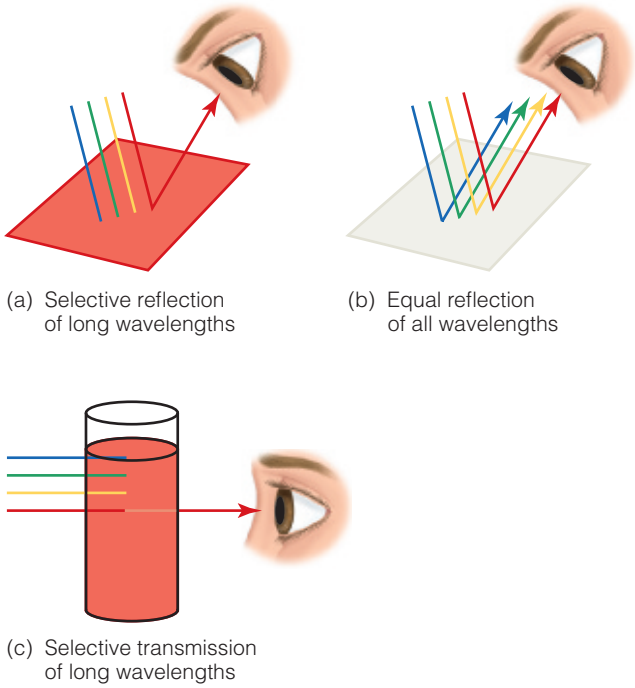
(a) Selective reflection of long wavelengths
(b) Equal reflection of all wavelengths
(c) Selective transmission of long wavelengths

Figure 9.5 (a) White light contains all of the wavelengths of the spectrum. A beam of white light is symbolized here by showing beams with wavelengths associated with blue, green, yellow, and red. When white light hits the surface of the paper, the long-wavelength light is selectively reflected and the rest of the wavelengths are absorbed. We therefore perceive the paper as looking red. (b) When all of the wavelengths are reflected equally, we see white. (c) In this example of selective transmission, the long-wavelength light is transmitted and the other wavelengths are absorbed by the liquid.

each selectively reflects more light in one part of the spectrum. Tomatoes predominantly reflect long wavelengths of light into our eyes, whereas lettuce principally reflects medium wavelengths. As a result, tomatoes appear red, whereas lettuce appears green. You can also contrast the reflectance curves for the lettuce and tomato with the curves for the achromatic (black, gray, and white) pieces of paper in **Figure 9.6b**, which are relatively flat, indicating equal reflectance across the spectrum. The difference between black, gray, and white is related to the overall amount of light reflected from an object. The black paper in Figure 9.6b reflects less than 10 percent of the light that hits it, whereas the white paper reflects more than 80 percent of the light.

Although most colors in the environment are created by the way objects selectively reflect some wavelengths, the color of things that are transparent, such as liquids, plastics, and glass, is created by selective transmission. Selective transmission means that only some wavelengths *pass through* the object or substance (**Figure 9.5c**). For example, cranberry juice selectively transmits long-wavelength light and appears red, whereas limeade selectively transmits medium-wavelength light and appears green. Transmission curves—plots of the percentage of light transmitted at each wavelength—look similar to the reflectance curves in Figure 9.6, but with percent transmission

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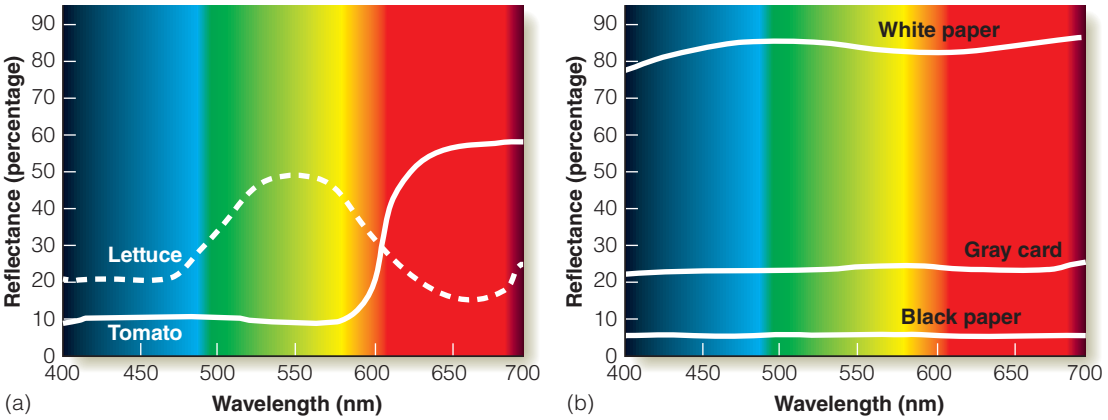

Figure 9.6 Reflectance curves for (a) lettuce and tomatoes (adapted from Williamson & Cummins, 1983) and (b) white, gray, and black paper (adapted from Clulow, 1972).

Table 9.1 Predominant Wavelengths Reflected or Transmitted and Perceived Color

WAVELENGTHS REFLECTED OR TRANSMITTED	PERCEIVED COLOR
Short	Blue
Medium	Green
Long and medium	Yellow
Long	Red
Long, medium, and short	White

plotted on the vertical axis. **Table 9.1** indicates the relationship between the wavelengths reflected or transmitted and the color perceived.

Color Mixing

The idea that the color we perceive depends largely on the wavelengths of light that reach our eyes provides a way to explain what happens when we mix different colors together. We will describe two ways of mixing colors: mixing paints and mixing lights.

Mixing Paints In kindergarten you learned that mixing yellow and blue paints results in green. Why is this so? Consider the blobs of paint in **Figure 9.7a**. The blue blob absorbs long-wavelength light and reflects some short-wavelength light and some medium-wavelength light (see the reflectance curve for "blue paint" in **Figure 9.7b**). The yellow blob absorbs short-wavelength light and reflects some medium- and long-wavelength light (see the reflectance curve for "yellow paint" in Figure 9.7b).

The key to understanding what happens when colored paints are mixed together is that when mixed, *both paints still absorb the same wavelengths they absorbed when alone, so the only wavelengths reflected are those that are reflected by both paints in common.*

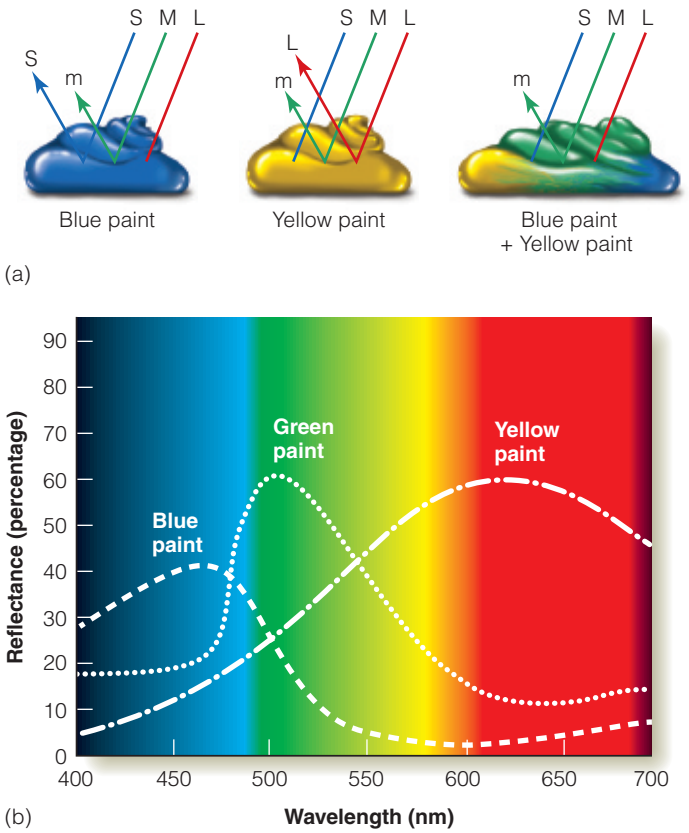

Figure 9.7 Color mixing with paint. Mixing blue paint and yellow paint creates a paint that appears green. This is subtractive color mixing.

So, as indicated in **Table 9.2**, a blob of blue paint absorbs all of the long-wavelength light, while a blob of yellow paint absorbs all of the short-wavelength light. Mix them together and the only wavelengths that survive all this absorption are some of the medium-wavelengths, which are associated with green. Because the blue and yellow blobs subtract all of

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Table 9.2 Mixing Blue and Yellow Paints (Subtractive Color Mixture)

Parts of the spectrum that are absorbed and reflected by blue and yellow paint. Wavelengths that are reflected from the mixture are highlighted. Light that is usually seen as green is the only light that is reflected in common by both paints.

	WAVELENGTHS		
	SHORT	MEDIUM	LONG
Blob of blue paint	Reflects all	Reflects some	Absorbs all
Blob of yellow paint	Absorbs all	Reflects some	Reflects some
Mixture of blue and yellow blobs	Absorbs all	**Reflects some**	Absorbs all

the wavelengths except some that are associated with green, mixing paints is called **subtractive color mixture**.

The reason that mixing blue and yellow paints results in green is that both paints reflect some light in the green part of the spectrum (notice that the overlap between the blue and yellow paint curves in Figure 9.7b coincides with the peak of the reflectance curve for green paint). If our blue paint had reflected only short wavelengths and our yellow paint had reflected only medium and long wavelengths, these paints would reflect no color in common, so mixing them would result in little or no reflection across the spectrum, and the mixture would appear black. Like objects, however, most paints reflect a band of wavelengths. If paints didn't reflect a range of wavelengths, then many of the color-mixing effects of paints that we take for granted would not occur.

Mixing Lights Let's now think about what would happen if we mix together blue and yellow lights. If a light that appears blue is projected onto a white surface and a light that appears yellow is projected on top of the light that appears blue, the area where the lights are superimposed is perceived as *white* (**Figure 9.8**). Given your lifelong knowledge that yellow and blue make green, and our discussion of paints above, this result may surprise you. But you can understand why this occurs by considering the wavelengths that are reflected into the eye by a mixture of blue and yellow lights. Because the two spots of light are projected onto a white surface, which reflects all wavelengths, all of the wavelengths that hit the surface are reflected into an observer's eyes (see the reflectance curve for white paper in Figure 9.5). The blue spot consists of a band of short wavelengths, so when it is projected alone, the short-wavelength light is reflected into the observer's eyes (**Table 9.3**). Similarly, the yellow spot consists of medium and long wavelengths, so when presented alone, these wavelengths are reflected into the observer's eyes.

The key to understanding what happens when colored lights are superimposed is that *all of the light that is reflected from the surface by each light when alone is also reflected when the lights are superimposed*. Thus, where the two spots are superimposed, the light from the blue spot and the light from the yellow spot are both reflected into the observer's eye. The added-together light therefore contains short, medium, and long wavelengths, as shown in **Figure 9.9**, which results in the perception of white. Because mixing lights involves adding up the wavelengths of each light in the mixture, mixing lights is called an **additive color mixture**.

We can summarize the connection between wavelength and color as follows:

- Colors of *light* are associated with wavelengths in the visible spectrum.
- The colors of *objects* are associated with which wavelengths are *reflected* (for opaque objects) or *transmitted* (for transparent objects).
- The colors that occur when we mix colors are also associated with which wavelengths are reflected into the eye. Mixing *paints* causes fewer wavelengths to be reflected (each paint *subtracts* wavelengths from the mixture); mixing *lights* causes more wavelengths to be reflected (each light *adds* wavelengths to the mixture).

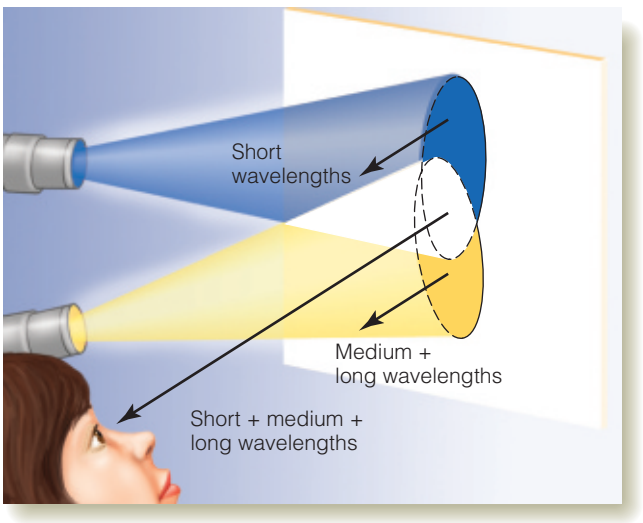

Figure 9.8 Color mixing with light. Superimposing a blue light and a yellow light creates the perception of white in the area of overlap. This is additive color mixing.

Table 9.3 Mixing Blue and Yellow Lights (Additive Color Mixture)

Parts of the spectrum that are reflected from a white surface for blue and yellow spots of light projected onto the surface. Wavelengths that are reflected from the mixture are highlighted.

	WAVELENGTHS		
	SHORT	MEDIUM	LONG
Spot of blue light	Reflected	No reflection	No reflection
Spot of yellow light	No reflection	Reflected	Reflected
Overlapping blue and yellow spots	**Reflected**	**Reflected**	**Reflected**

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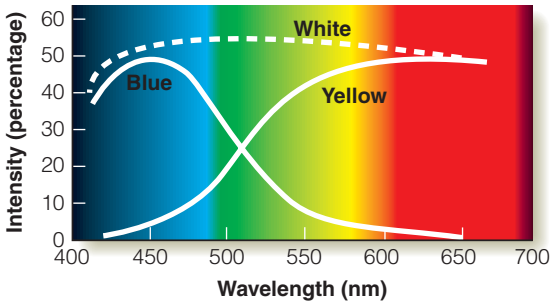

Figure 9.9 Spectral distribution of blue and yellow light. The dashed curve, which is the sum of the blue and yellow distributions, is the wavelength distribution for white light. Thus when blue and yellow lights are superimposed, the wavelengths add and the result is the perception of white.

We will see later in the chapter that wavelength is not the whole story when it comes to color perception. For example, our perception of an object's color can be influenced by the background on which the object is seen, by the colors observers are exposed to the environment, and by how viewers interpret how a scene is illuminated. But for now our main focus is on the connection between wavelength and color.

9.3 Perceptual Dimensions of Color

Isaac Newton described the visible spectrum (Figure 9.4b) in his experiments in terms of seven colors: red, orange, yellow, green, blue, indigo, and violet. His use of seven color terms probably had more to do with mysticism than science, however, as he wanted to harmonize the visible spectrum (seven colors) with musical scales (seven notes), the passage of time (seven days in a week), astronomy (there were seven known planets at the time), and religion (seven deadly sins).

Modern vision scientists tend to exclude indigo from the list of **spectral colors** because humans actually have a difficult time distinguishing it from blue and violet. There are also many **nonspectral colors**—colors that do not appear in the spectrum because they are mixtures of other colors, such as magenta (a mixture of blue and red). Ultimately, the number of colors we can differentiate is enormous: If you've ever decided to paint your bedroom wall, you will have discovered a dizzying number of color choices in the paint department of your local home improvement store. In fact, major paint manufacturers have thousands of colors in their catalogs, and your computer monitor can display millions of different colors. Although estimates of how many colors humans can discriminate vary widely, a conservative estimate is that we can tell the difference between about 2.3 million different colors (Linhares et al., 2008).

How can we perceive millions of colors when we can describe the visible spectrum in terms of only six or seven colors? The answer is that there are three perceptual dimensions

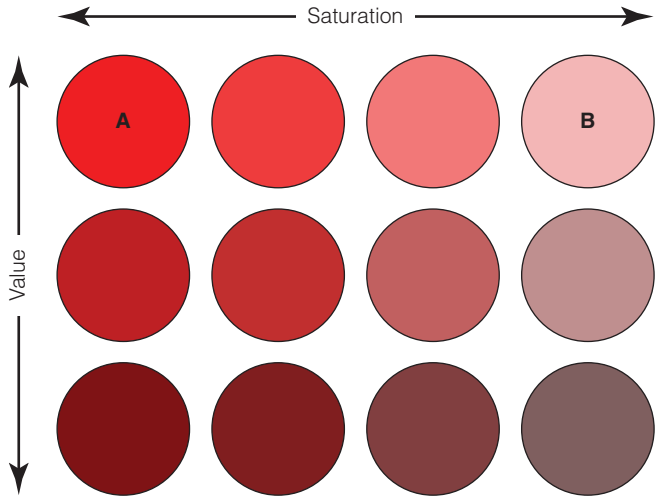

Figure 9.10 These 12 color patches have the same hue (red). Saturation decreases from left to right. Lightness decreases from top to bottom.

of color, which together can create the large number of colors we can perceive. We previously called colors like blue, green, and red *chromatic colors*. Another term for these colors is **hues**. **Figure 9.10** shows a number of color patches, most of which we would describe as having a red hue. What makes these colors appear different is their variation in the other two dimensions of color, *saturation* and *value* (also called *lightness*).

Saturation refers to the intensity of color. Moving from left to right in Figure 9.10, progressively more white has been added to each color patch and, as a result, saturation decreases. When hues become **desaturated**, they can take on a faded or washed-out appearance. For example, color patch A in Figure 9.10 appears to be a deep and vivid red, but color patch B appears to be a desaturated muted pink. **Value** or **lightness** refers to the light-to-dark dimension of color. Moving down the columns in Figure 9.10, value decreases as the colors become darker.

Another useful way to illustrate the relationship among hue, saturation, and value is to arrange colors systematically within a three-dimensional color space called a **color solid**. **Figure 9.11a** depicts the dimensions of hue, saturation, and value in the **Munsell color system**, that was developed by Albert Munsell in the early 1900s and is still in wide use today.

Different hues are arranged around the circumference of the cylinder with perceptually similar hues placed next to each other. Notice that the order of the hues around the cylinder matches the order of the colors in the visible spectrum shown in Figure 9.4b. Saturation is depicted by placing more saturated colors toward the outer edge of the cylinder and more desaturated colors toward the center. Value is represented by the cylinder's height, with lighter colors at the top and darker colors at the bottom. The color solid therefore creates a coordinate system in which our perception of any color can be defined by hue, saturation, and value.

Now that we have introduced the basic properties of color and color mixing, we are going to focus on the connection between color vision and the cone receptors in the retina.

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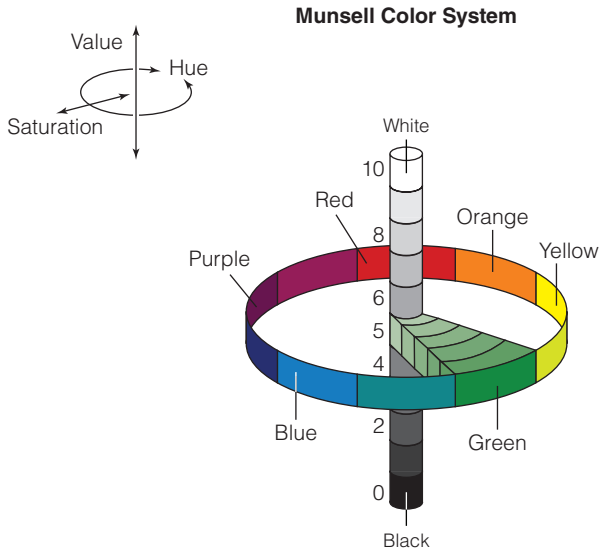

Figure 9.11 The Munsell color space. Hue is arranged in a circle around the vertical, which represents value. Saturation increases with distance away from the vertical.

TEST YOURSELF 9.1

1. Describe the case of Mr. I. What does it illustrate about color perception?
2. What are the various functions of color vision?
3. What physical characteristic of light is most closely associated with color perception? How is this demonstrated by differences in reflection and transmission of light of different objects?
4. Describe subtractive and additive color mixing. How can the results of these two types of color mixing be related to the wavelengths that are reflected into an observer's eyes?
5. What are spectral colors? Nonspectral colors? How many different colors can humans discriminate?
6. What are hue, saturation, and value? Describe how the Munsell color system represents different properties of color.

9.4 The Trichromacy of Color Vision

We now shift to physiology, and begin with the retina and physiological principles that are based on wavelength.

A Little History

We begin by discussing the retinal basis of color vision by returning to Isaac Newton's prism experiment (Figure 9.4). When Newton separated white light into its components to reveal the visible spectrum, he argued that each component of the spectrum must stimulate the retina differently in order for us to perceive color. He proposed that "rays of light in falling upon the bottom of the eye excite vibrations in the retina. Which vibrations, being propagated along the fibres of the optick nerves into the brain, cause the sense of seeing" (Newton, 1704). We know now that electrical signals, not "vibrations," are what is transmitted down the optic nerve to the brain, but Newton was on the right track in proposing that activity associated with different lights gives rise to the perceptions of different colors.

About 100 years later, the British physicist Thomas Young (1773–1829), starting with Newton's proposed vibrations, suggested that Newton's idea of a link between each size of vibration and each color won't work, because a particular place on the retina can't be capable of the large range of vibrations required. His exact words were: "Now, as it is almost impossible to conceive of each sensitive point on the retina to contain an infinite number of particles, each capable of vibrating in perfect unison with every possible undulation, it becomes necessary to suppose the number limited, for instance, to the three principal colors, red, yellow, and blue" (Young, 1802).

The actual quote from Young is included here because it is so important. It is this proposal—that color vision is based on *three* principal colors—that marks the birth of what is today called the **trichromacy of color vision**, which in modern terminology states that color vision depends on the activity of three different receptor mechanisms. At the time it was proposed, however, Young's theory was little more than an insightful idea that, if correct, would provide an elegant solution to the puzzle of color perception. Young had little interest in conducting experiments to test his ideas, however, and never published any research to support his theory (Gurney, 1831; Mollon, 2003; Peacock, 1855). Thus, it was left to James Clerk Maxwell (1831–1879) and Hermann von Helmholtz (whose proposal of unconscious inference we discussed in Chapter 5) to provide the needed experimental evidence for trichromatic theory (Helmholtz, 1860; Maxwell, 1855). Although Maxwell conducted his experiments before Helmholtz, Helmholtz's name became attached to Young's idea of three receptors, and trichromatic theory became known as the **Young-Helmholtz theory**. That trichromatic theory became known as the Young-Helmholtz theory rather than the Young-Maxwell theory has been attributed to Helmholtz's prestige in the scientific community and to the popularity of his *Handbook of Physiology* (1860), in which he described the idea of three receptor mechanisms (Heesen, 2015; Sherman, 1981).

Even though Maxwell was denied "naming rights" for his discoveries in color vision, if it is any consolation to him, a 1999 poll of leading physicists named him the third greatest physicist of all time, behind only Newton and Einstein, for his work in electromagnetism (Durrani & Rogers, 1999). It is also Maxwell's critical color-matching experiments that we will describe in detail in the next section as we begin to consider the evidence for trichromatic theory.

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Color-Matching Evidence for Trichromacy

The trichromacy of color vision is supported by the results of a psychophysical procedure called **color matching**.

METHOD | Color Matching

The procedure used in a color matching experiment is shown in Figure 9.12. The experimenter presents a reference color that is created by shining a single wavelength of light on a "reference field". The observer then matches the reference color by mixing different wavelengths of light in a "comparison field". In this example, the observer is shown a 500-nm light in the reference field on the left and then asked to adjust the amounts of 420-nm, 560-nm, and 640-nm lights in the comparison field on the right, until the perceived color of the comparison field matches the reference field.

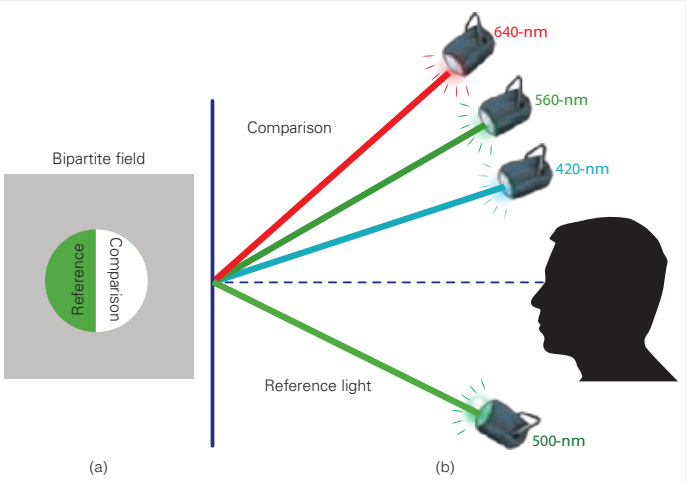

Figure 9.12 A color matching experiment. (a) The observer's view of the bipartite field. The comparison field is empty here, but becomes colored when (b) the observer adjusts the amount of three wavelengths to create a color that matches the color in the reference field.

The key finding from Maxwell's color-matching experiments was that any reference color could be matched provided that observers were able to adjust the *proportions* of *three* wavelengths in the comparison field. Two wavelengths allowed participants to match some, but not all, reference colors, and they never needed four wavelengths to match any reference color.

Based on the finding that people with normal color vision need at least three wavelengths to match any other wavelength, Maxwell reasoned that color vision depends on three receptor mechanisms, each with different spectral sensitivities. (Remember from Chapter 3 that spectral sensitivity indicates the sensitivity to wavelengths in the visible spectrum, as shown in Figure 3.15 on page 50.) According to trichromatic theory, light of a particular wavelength stimulates each receptor mechanism to different degrees, and the pattern of activity in the three mechanisms results in the perception of a color. Each wavelength is therefore represented in the nervous system by its own pattern of activity in the three receptor mechanisms.

The story of the physiology of trichromacy is a story of delayed gratification, because almost 100 years passed between the proposal of three receptor mechanisms and actually demonstrating their physiological existence.

Measuring the Characteristics of the Cone Receptors

In 1963 and 1964 a number of research teams made a discovery that provided physiological support for the trichromacy that was based on the results of Maxwell's color matching experiments. The discovery of three types of cones in the human retina was made using the technique of **microspectrophotometry**, which made it possible to direct a narrow beam of light into a single cone receptor. By presenting light at wavelengths across the spectrum, it was determined that there were three types of cones, with the absorption spectra shown in **Figure 9.13**.

The short-wavelength pigment (S), absorbed maximally at 419-nm; the middle-wavelength pigment (M), at 531-nm; and the long-wavelength pigment (L), at 558-nm (Brown & Wald, 1964; Dartnall et al., 1983; Marks et al., 1964).

The reaction of vision researchers to these measurements was interesting. On one hand, the measurements of the cone spectra were hailed as an impressive and important achievement. On the other hand, because of the results of the color matching experiments done almost 100 years earlier, some said "we knew it all along." But the new measurements were important because they were not only consistent with trichromacy as predicted by color matching, but they also revealed the exact spectra of the three cone mechanisms, and, unexpectedly, revealed the large overlap between the L and M cones.

Another advance in describing the cones was provided by a technique called **adaptive optical imaging**, which made it possible to look into a person's eye and take pictures that showed how the cones are arranged on the surface of the retina. This was an impressive achievement, because the eye's cornea and lens contain imperfections called **aberrations** that distort the light on its way to the retina. This means that when your optometrist or ophthalmologist uses an ophthalmoscope to look into your eye, they can see blood vessels and the surface of the retina, but the image is too blurry to make out individual receptors.

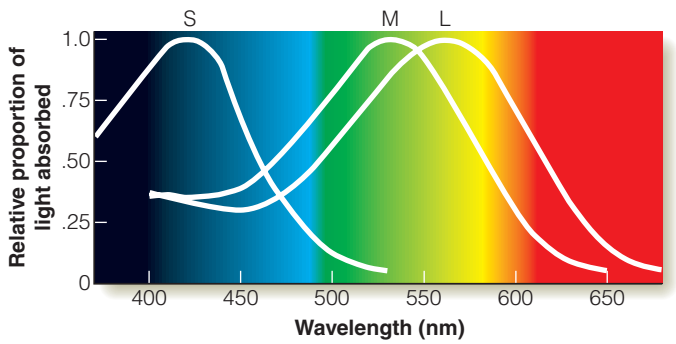

Figure 9.13 Absorption spectra of the three cone pigments. (From Dartnall et al., 1983)

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Adaptive optical imaging creates a sharp image by first measuring how the optical system of the eye distorts the image reaching the retina, and then taking a picture through a deformable mirror that cancels the distortion created by the eye. The result is a clear picture of the **cone mosaic** like the one in **Figure 9.14**, which shows foveal cones. In this picture the cones are colored to distinguish the short-, medium-, and long-wavelength cones.

Figure 9.15 shows the relationship between the responses of the three kinds of receptors derived from the absorption spectrum, and the perception of different colors. In this figure, the responses in the S, M, and L receptors are indicated by the size of the receptors. For example, short-wavelength light, which appears blue in the spectrum, is signaled by a large response in the S receptor, a smaller response in the M receptor, and an even smaller response in the L receptor. Yellow is signaled by a very small response in the S receptor and large responses in the M and L receptors. White is signaled by equal activity in all the receptors.

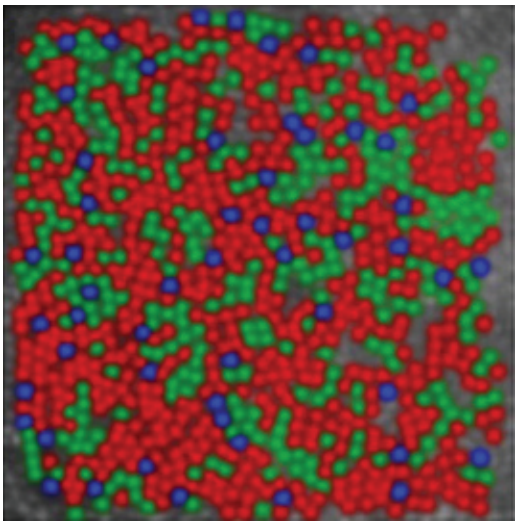

Figure 9.14 Cone mosaic showing long- (red), medium- (green), and short-wavelength (blue) cones in the fovea. The colors were added after the images were created. (From Roorda & Williams, 1999)

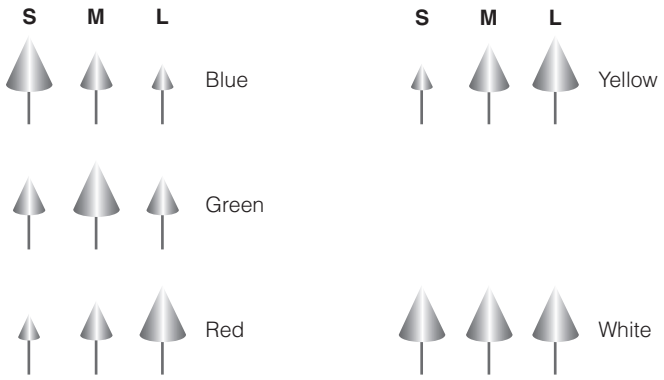

Figure 9.15 Patterns of firing of the three types of cones to wavelengths associated with different colors. The size of the cones symbolizes the amount of activity in the short-, medium-, and long-wavelength cones.

The patterns of activity shown in Figure 9.15 indicate how different wavelengths of light activate the three types of cone receptors. Later in this chapter, we will see that this link between wavelength and receptor activity is only part of the story of color vision, because our perception of color is also affected by factors such as our state of adaptation, the nature of our surroundings, and our interpretation of the illumination. However, for now we will continue the story of the connection between color perception and the activity of cones by returning to the color-matching results that led to the proposal of trichromatic theory.

The Cones and Trichromatic Color Matching

Remember that in a color-matching experiment, a wavelength in one field is matched by adjusting the proportions of three different wavelengths in another field (Figure 9.12). This result is interesting because the lights in the two fields are physically different (they contain different wavelengths) but they are perceptually identical (they look the same). This situation, in which two physically different stimuli are perceptually identical, is called **metamerism**, and the two identical fields in a color-matching experiment are called **metamers**.

The reason metamers look alike is that they both result in the same pattern of response in the three cone receptors. For example, when the proportions of a 620-nm red light that looks red and a 530-nm green light that looks green are adjusted so the mixture matches the color of a 580-nm light, which looks yellow, the two mixed wavelengths create the same pattern of activity in the cone receptors as the single 580-nm light (**Figure 9.16**). The 530-nm green light causes a large response in the M receptor, and the 620-nm red light causes a large response in the L receptor. Together, they result in a large response in the M and L receptors and a much smaller response in the S receptor. This is the pattern for yellow and is the same as the pattern generated by the 580-nm light. Thus,

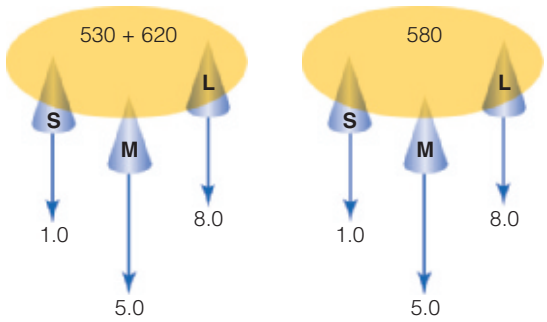

Figure 9.16 Principle behind metamerism. The proportions of 530-nm and 620-nm lights in the field on the left have been adjusted so that the mixture appears identical to the 580-nm light in the field on the right. The numbers indicate the responses of the short-, medium-, and long-wavelength receptors. There is no difference in the responses of the two sets of receptors, so the two fields are perceptually indistinguishable.

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even though the lights in these two fields are *physically different*, the two lights result in identical physiological responses so they are identical as far as the brain is concerned and they are therefore perceived as being the same.

One way to appreciate the connection between the results of color matching experiments and cone pigments is to consider what happens to color perception when there are fewer than three types of receptors. We begin by considering what happens when there is only a single type of receptor.

Color Vision With Only One Pigment: Monochromacy

Monochromatism is a rare form of color blindness that is usually hereditary and occurs in only about 10 people out of 1 million (LeGrand, 1957). **Monochromats** usually have no functioning cones, so their vision is created only by the rods. Their vision, therefore, has the characteristics of rod vision in both dim and bright lights so they see only in shades of lightness (white, gray, and black) and can therefore be called **color blind**. A person with normal color vision can experience what it is like to be a monochromat by sitting in the dark for several minutes. When dark adaptation is complete (see Figure 3.13), vision is controlled by the rods, which causes the world to appear in shades of gray.

Because monochromats perceive all wavelengths as shades of gray, they can match any wavelength by picking another wavelength and adjusting its intensity. Thus, a monochromat needs only one wavelength to match any wavelength in the spectrum. We can understand why color vision is not possible in a person with just one receptor type by considering how a person with just one pigment would perceive two lights, one 480 nm and one 600 nm, which a person with normal color vision sees as blue and red, respectively. The absorption spectrum for the single pigment, shown in **Figure 9.17a**, indicates that the pigment absorbs 10 percent of 480-nm light and 5 percent of 600-nm light.

To discuss what happens when our one-pigment observer looks at the two lights, we have to return to our description of visual pigments in Chapter 3 (see page 45). Remember that when light is absorbed by the *retinal* part of the visual pigment molecule, the retina changes shape, a process called *isomerization*. (Although we will usually specify light in terms of its wavelength, light can also be described as consisting of small packets of energy called *photons*, with one photon being the smallest possible packet of light energy.) The visual pigment molecule isomerizes when the molecule absorbs one photon of light. This isomerization activates the molecule and triggers the process that activates the visual receptor and leads to seeing the light.

If the intensity of each light is adjusted so 1,000 photons of each light enter our one-pigment observer's eyes, we can see from **Figure 9.17b** that the 480-nm light isomerizes $1{,}000 \times 0.10 = 100$ visual pigment molecules and the 600-nm light isomerizes $1{,}000 \times 0.05 = 50$ molecules. Because the 480-nm light isomerizes twice as many visual pigment molecules as the

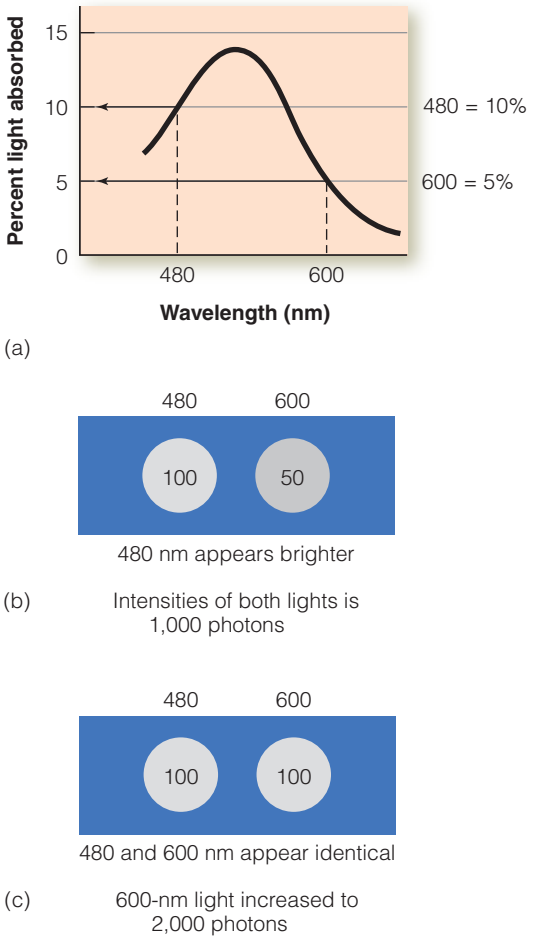

Figure 9.17 (a) Absorption spectrum of a visual pigment that absorbs 10 percent of 480-nm light and 5 percent of 600-nm light. (b) Visual pigment molecules isomerized when the intensity of both 480-nm and 600-nm lights is 1,000, determined by multiplying intensity times the percent of light absorbed. Because more visual pigments are isomerized by the 480-nm light, it will appear brighter. (c) Molecules isomerized when the intensity of the 480-nm light is 1,000 and the intensity of the 600-nm light is 2,000. In this case, both lights will look identical.

600-nm light, it will cause a larger response in the receptor, resulting in perception of a brighter light. But if we increase the intensity of the 600-nm light to 2,000 photons, as shown in **Figure 9.17c**, then this light will also isomerize 100 visual pigment molecules.

When the 1,000 photon 480-nm light and the 2,000 photon 600-nm light both isomerize the same number of molecules, the result will be that the two spots of light will appear identical. The difference in the wavelengths of light doesn't matter, because of the **principle of univariance**, which states that once a photon of light is absorbed by a visual pigment molecule, the identity of the light's wavelength is lost. An isomerization is an isomerization no matter what wavelength caused it. Univariance means that the receptor does not know the *wavelength* of light it has absorbed, only the *total amount* it has absorbed. Thus, by adjusting the intensities of the two lights, we can

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cause the single pigment to result in identical responses, so the lights will appear the same even though their wavelengths are different.

What this means is that a person with only one visual pigment can match any wavelength in the spectrum by adjusting the *intensity* of any other wavelength and sees all of the wavelengths as shades of gray. Thus, adjusting the intensity appropriately can make the 480-nm and 600-nm lights (or any other wavelengths) look identical.

The message of our one-pigment example is that a person needs more than one type of receptor to perceive chromatic color. We now consider what happens when there are two types of cones.

Color Vision With Two Pigments: Dichromacy

Let's consider what happens when the retina contains two pigments with absorption spectra shown by the dashed curves in **Figure 9.18**. Considering the ratios of responses to two wavelengths we can see that the 480-nm light causes a large response from pigment 1 and a smaller response from pigment 2, and that the 600-nm light causes a larger response in pigment 2 and a smaller response in pigment 1. These ratios remain the same no matter what the light intensities. The ratio of the response of pigment 1 to pigment 2 is always 10 to 2 for the 480-nm light and 5 to 10 for the 600-nm light. Thus, just as in the case when there are three pigments, the visual system can use ratio information such as this to identify the wavelength of any light.

According to this reasoning, two pigments should provide information about which wavelength is present. People with just two types of cone pigment, called dichromats, see chromatic colors, just as our calculations predict, but because they have only two types of cones, they confuse some colors that trichromats can distinguish.

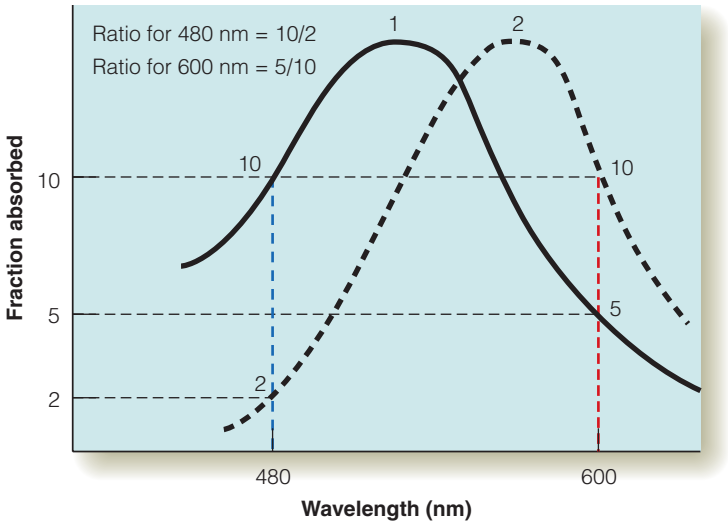
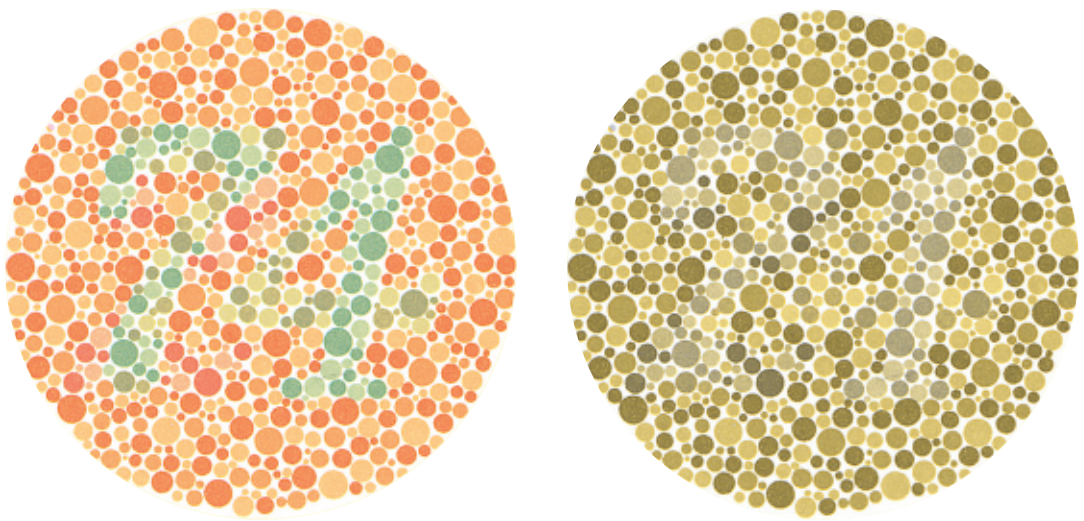


Figure 9.18 Adding a second pigment (dashed curve) to the one in Figure 9.17. Now the 480-nm and 600-nm lights can be identified by the ratio of response in the two pigments. The ratio for the 480-nm light is 10/2. The ratio for the 600-nm light is 5/10. These ratios occur no matter what the intensity of the light.

A dichromat, like our two-pigment observer in Figure 9.16, needs only two wavelengths to match any other wavelength in the spectrum. Thus, one way to determine the presence of color deficiency is by using the color-matching procedure to determine the minimum number of wavelengths needed to match any other wavelength in the spectrum.

Another way to diagnose color deficiency is by a color vision test that uses stimuli called Ishihara plates. An example plate is shown in **Figure 9.19a**. In this example, people with normal color vision see the number "74," but people with a form of red–green color deficiency might see something like the depiction in **Figure 9.19b**, in which the "74" is not visible.

Figure 9.19 (a) An example of an Ishihara plate for testing color deficiency. A person with normal color vision sees a "74" when the plate is viewed under standardized illumination. (b) The same Ishihara plate as perceived by a person with a form of red–green color deficiency.



(a) (b)

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Once we have determined that a person's vision is color deficient, we are still left with the question: What colors does a dichromat see compared to a trichromat? To determine what a dichromat perceives compared to a trichromat, we need to locate a **unilateral dichromat**—a person with trichromatic vision in one eye and dichromatic vision in the other. Both of the unilateral dichromat's eyes are connected to the same brain, so this person can look at a color with his dichromatic eye and then determine which color it corresponds to in his trichromatic eye. Although unilateral dichromats are extremely rare, the few who have been tested have helped us determine the nature of a dichromat's color experience (Alpern et al., 1983; Graham et al., 1961; Sloan & Wollach, 1948). Let's now look at the three kinds of dichromats and the nature of their color experience.

There are three major forms of **dichromatism**: *protanopia*, *deuteranopia*, and *tritanopia*. The two most common kinds, protanopia and deuteranopia, are inherited through a gene located on the X chromosome (Nathans et al., 1986). Males (XY) have only one X chromosome, so a defect in the visual pigment gene on this chromosome causes color deficiency. Females (XX), on the other hand, with their two X chromosomes, are less likely to become color deficient because only one normal gene is required for normal color vision. These forms of color vision are therefore called sex-linked because women can carry the gene for color deficiency without being color deficient themselves. Thus, many more males than females are dichromats.

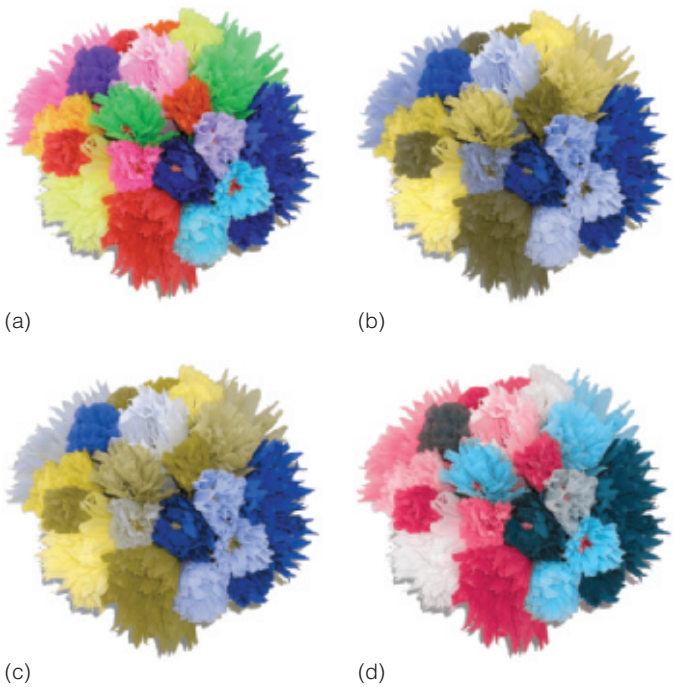

Figure 9.20 How colored paper flowers appear to (a) trichromats, (b) protanopes, (c) deuteranopes, and (d) tritanopes. (Photograph by Bruce Goldstein; color processing courtesy of Jay Neitz and John Carroll)

As we describe what the three types of dichromats perceive, we use as our reference points **Figures 9.20a** and **9.21a**, which show how a trichromat perceives a bunch of colored paper flowers and the visible spectrum, respectively.

- **Protanopia** affects 1 percent of males and 0.02 percent of females and results in the perception of colors shown in **Figure 9.20b**. A protanope is missing the long-wavelength pigment. As a result, a protanope perceives short-wavelength light as blue, and as the wavelength is increased, the blue becomes less and less saturated until, at 492 nm, the protanope perceives gray (**Figure 9.21b**). The wavelength at which the protanope perceives gray is called the **neutral point**. At wavelengths above the neutral point, the protanope perceives yellow, which becomes less intense at the long wavelength end of the spectrum.
- **Deuteranopia** affects about 1 percent of males and 0.01 percent of females and results in the perception of color in **Figure 9.20c**. A deuteranope is missing the medium-wavelength pigment. A deuteranope perceives blue at short wavelengths, sees yellow at long wavelengths, and has a neutral point at about 498 nm (**Figure 9.21c**) (Boynton, 1979).
- **Tritanopia** is very rare, affecting only about 0.002 percent of males and 0.001 percent of females.

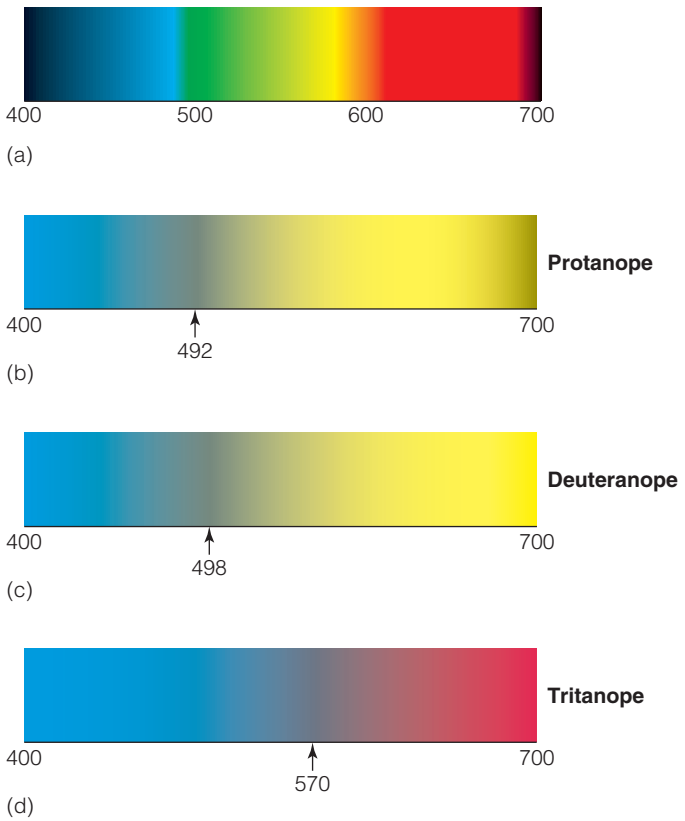

Figure 9.21 How the visible spectrum appears to (a) trichromats, (b) protanopes, (c) deuteranopes, and (d) tritanopes. The number indicates the wavelength of the neutral point. (Spectra courtesy of Jay Neitz and John Carroll)

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A tritanope is missing the short-wavelength pigment. A tritanope sees colors as in **Figure 9.20d** and sees the spectrum as in **Figure 9.21d**—blue at short wavelengths, red at long wavelengths, and a neutral point at 570 nm (Alpern et al., 1983).

In addition to monochromatism and dichromatism, there is one other prominent type of color deficiency called **anomalous trichromatism**. An anomalous trichromat needs three wavelengths to match any wavelength, just as a normal trichromat does. However, the anomalous trichromat mixes these wavelengths in different proportions from a trichromat, and an anomalous trichromat is not as good as a trichromat at discriminating between wavelengths that are close together.

The story we have been telling about the connection between the cone receptors and color vision has taken place exclusively in the receptors in the retina. But there's more to color vision than what's happening in the receptors because signals from the receptors travel through the retina and out the back of the eye to the lateral geniculate nucleus, then to the visual cortex, and finally to other areas of the cortex. One result of this further processing was noted by Ewald Hering (1834–1918) long before researchers began to understand the nature of this processing. Hering's insight was his description of the opponency of color vision.

TEST YOURSELF 9.2

1. What did Thomas Young say was wrong with Newton's idea that color is created by vibrations?
2. How did Young explain color vision? Why is his explanation called the Young-Helmholtz theory?
3. Describe Maxwell's color matching experiments. How did the results support the trichromacy of vision?
4. What is the connection between trichromacy and the cone receptors and pigments?
5. What is metamerism? How is it related to the results of color matching experiments?
6. What is monochromacy? How does a monochromat match lights in a color matching experiment? Does a monochromat perceive chromatic color?
7. What is the principle of univariance? How does the principle of univariance explain the fact that a monochromat can match any wavelength in the spectrum by adjusting the intensity of any other wavelength?
8. Describe how pigment absorption spectra can explain how wavelength can be determined if there are only two receptor types.
9. How would color matching results differ for a person with two types of cone receptors, compared to three?
10. What is dichromacy? What procedure was used to determine how a dichromat's color vision compared to a trichromat's?
11. What are the three types of dichromacy?

9.5 The Opponency of Color Vision

What does opponency mean? For color vision, it means that there are pairs of colors that have opponent, or opposite, responses. Hering's theory, called the **opponent-process theory of color vision**, stated that there are two pairs of chromatic colors, red–green and blue–yellow (Hering, 1878, 1964). He picked these pairs of colors based on phenomenological observations—observations in which observers described the colors they were experiencing.

Behavioral Evidence for Opponent-Process Theory

There are two types of behavioral evidence for opponent-process theory: phenomenological and psychophysical.

Phenomenological Evidence Phenomenological evidence, which is based on color *experience*, was central to Hering's proposal of opponent-process theory. His ideas about opponent colors were based on people's color experiences when looking at a *color circle* like the one in **Figure 9.22**. A **color circle** arranges perceptually similar colors next to each other around its perimeter just like the color solid depicted in Figure 9.11. Another property of the color circle is that

Figure 9.22 The color circle described by Hering. Colors on the left appear blueish, colors on the right appear yellowish, colors on the top appear reddish, and colors on the bottom appear greenish. Lines connect opponent colors.

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colors across from each other are complementary colors—colors which when combined cancel each other to create white or gray. The difference between a color circle and a color solid is simply that the color circle focuses only on hue, without considering variations in saturation or value.

Hering identified four **primary colors**—red, yellow, green, and blue—and proposed that each of the other colors are made up of combinations of these primary colors. This was demonstrated using a procedure called **hue scaling**, in which participants were given colors from around the hue circle and told to indicate the proportions of red, yellow, blue, and green that they perceived in each color. One result was that each of the primaries was "pure." For example, there is no yellow, blue, or green in the red. The other result was that each of the intermediate colors like purple or orange were judged to contain mixtures of two or more of the primaries. Results such as these led Hering to call the primary colors **unique hues**.

Hering proposed that our color experience is built from the four primary chromatic colors arranged into two opponent pairs: yellow–blue and red–green. To these chromatic colors, Hering also considered black and white to be an opponent achromatic pair.

Ingenious as Hering's opponent-mechanism proposal was, the theory wasn't widely accepted, for three reasons: (1) its main competition, trichromatic theory, was championed by Helmholtz, who had great prestige in the scientific community; (2) Hering's phenomenological evidence, which was based on describing the appearance of colors, could not compete with Maxwell's quantitative color mixing data; and (3) there was no neural mechanism known at that time that could respond in opposite ways.

Psychophysical Evidence The idea of opponency was given a boost in the 1950s by Leo Hurvich and Dorthea Jameson's (1957) **hue cancellation** experiments. The purpose of the hue cancelation experiments was to provide quantitative measurements of the strengths of the B–Y and R–G components of the opponent mechanisms. Let's consider how they used hue cancellation to determine the strength of the blue mechanism.

METHOD | Hue Cancellation

We begin with a 430-nm light, which appears blue. Leo Hurvich and Dorthea Jameson (1957) reasoned that since yellow is the opposite of blue and therefore cancels it, they could determine the amount of blueness in a 430-nm light by determining how much yellow needs to be added to cancel all perception of "blueness." The blue dot in **Figure 9.23** indicates the amount of yellow that was added to 430-nm light to cancel all "blueness." Once this is determined for the 430-nm light, the measurement is repeated for 440 nm and so on, across the spectrum, until reaching the wavelength where there is no blueness, indicated by the circle.

Hue cancelation was then used to determine the strength of the yellow mechanism by determining how much blue needs to be added to cancel yellowness at each wavelength. For red and green, the strength of the red mechanism is determined by measuring how much green needs to be added to cancel the perception of redness, and the strength of the green mechanism, by measuring how much red needs to be added to cancel the perception of greenness.

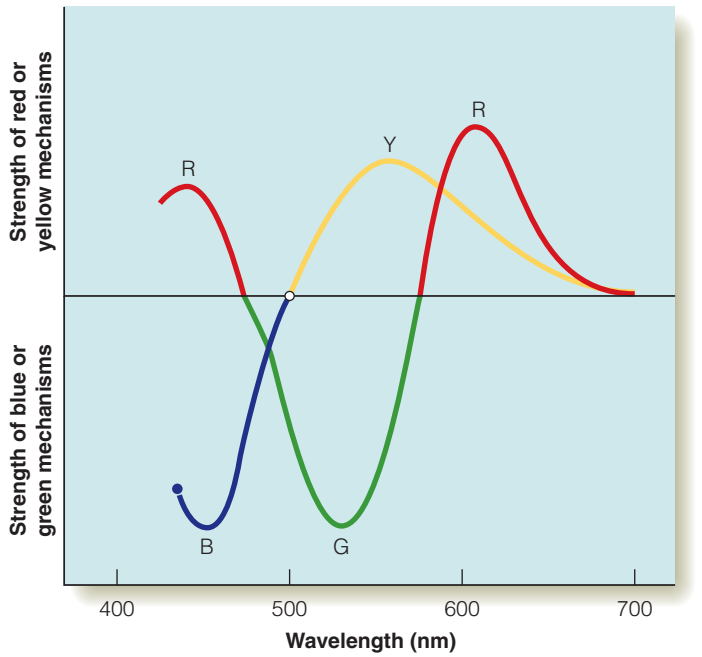

Figure 9.23 Results of Hurvich and Jameson's (1957) hue cancellation experiments. For the blue–yellow determinations, the blue curve is inverted to symbolize that blue is opponent to yellow, and for the red–green determinations, the green curve is inverted because green is opponent to red.

In Figure 9.23 the blue and green curves have been inverted to emphasize the fact that blue (plotted as negative in the figure) opposes yellow (plotted as positive) and that green (negative) opposes red (positive). These curves could just as well be reversed, with blue and green positive and red and yellow negative.

Hurvich and Jameson's hue cancellation experiments were an important step toward acceptance of opponent-process theory because they went beyond Hering's phenomenological observations by providing quantitative measurements of the strengths of the opponent mechanisms.

Physiological Evidence for Opponent-Process Theory

Even more crucial for the acceptance of opponent-process theory was the discovery of **opponent neurons** that responded with an excitatory response to light from one part of the spectrum and with an inhibitory response to light from another part (DeValois, 1960; Svaetichin, 1956).

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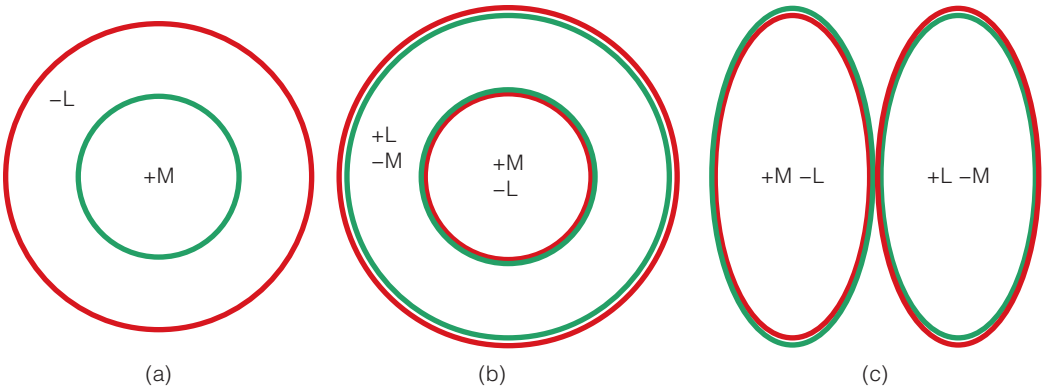

Figure 9.24 Receptive fields of (a) a circular single-opponent cortical neuron. This +M –L neuron has a center-surround receptive field. Its firing increases when a medium-wavelength light is presented to the center area of the receptive field and decreases when a long-wavelength light is presented to the surrounding area. (b) A circular double-opponent neuron. Firing increases to medium-wavelength light presented to the center, and to long-wavelength light presented to the surround. Firing decreases to long-wavelength light presented to the center and medium-wavelength light presented to the surround. (c) A side-by-side double-opponent cortical neuron. This neuron increases firing when a vertical medium-wavelength bar is presented to the left side and when a vertical long-wavelength bar is presented to the right side and decreases firing when a vertical long-wavelength bar is presented to the left side and when a vertical medium-wavelength bar is presented to the right side. (From Conway et al., 2010)

In an early paper that reported opponent neurons in the lateral geniculate nucleus of the monkey, Russell DeValois (1960) recorded from neurons that responded with an excitatory response to light from one part of the spectrum and with an inhibitory response to light from another part (also see Svaetichin, 1956). Later work identified opponent cells with different receptive field layouts. **Figure 9.24** shows three receptive field layouts: (a) circular single opponent, (b) circular double opponent, and (c) side-by-side single opponent (Conway et al., 2010).

The discovery of opponent neurons provided physiological evidence for the opponency of color vision. The circuits in **Figure 9.25** show how the opponent neurons can be created by inputs from the three cones. In **Figure 9.25a**, the L-cone sends excitatory input to a bipolar cell (see Chapter 3, page 51), whereas the M-cone sends inhibitory input to the cell. This creates an +L –M cell that responds with excitation to the long wavelengths that cause the L-cone to fire and with inhibition to the medium wavelengths that cause the M-cone to fire. **Figure 9.25b** shows how excitatory input from the M-cone and inhibitory input from the L-cone create an +M –L cell.

Figure 9.25c shows that the +S –ML cell also receives inputs from the cones. It receives an excitatory input from the S cone and an inhibitory input from cell A, which sums the inputs from the M and L cones. This arrangement makes sense if we remember that we perceive yellow when both the M and the L receptors are stimulated. Thus, cell A, which receives inputs from both of these receptors, causes the "yellow" response of the +S –ML mechanism. **Figure 9.25d** shows the connections among neurons forming the +ML –S (or +Y –B) cell. Opponent responding has also been observed in a number of cortical areas, including the visual receiving area (V1) (Gegenfurtner & Kiper, 2003; Nunez et al., 2018).

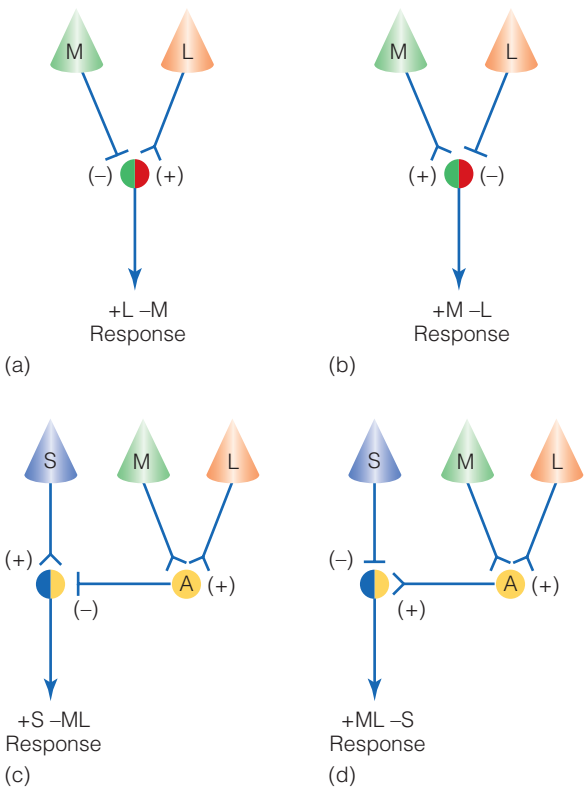

Figure 9.25 Neural circuits showing how (a) +L –M, (b) +M –L, (c) +S –ML, and (d) +ML –S mechanisms can be created by excitatory and inhibitory inputs from the three types of cone receptors.

Recent research has concluded that single-opponent cells like the ones in Figures 9.24a and 9.24c respond to large areas of color and double opponent cells like the one in Figure 9.24b respond to color patterns and borders (Nunez et al., 2018).

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Questioning the Idea of Unique Hues

The results of the hue-cancellation experiments and the discovery of opponent neurons were taken by researchers in the 1950s and 1960s as supporting Hering's opponent-process theory of vision. The fact that there are neurons that respond in opposite ways to different parts of the spectrum does support Hering's idea of opponency. However, remember that Hering also proposed that blue, yellow, red, and green are unique hues. The proposed specialness of unique hues led researchers who first recorded from opponent neurons to give them names like +B −Y and +R −G that corresponded to the unique hues. The implication of these labels is that these neurons are responsible for our perception of these hues. This idea has, however, been questioned by recent research.

One argument against the idea that there is a direct connection between the firing of opponent neurons and perceiving primary or unique hues is that the wavelengths that cause maximum excitation and inhibition don't match the wavelengths associated with the unique hues (Skelton et al., 2017). And returning to the hue scaling experiments we described earlier, recent research has repeated these experiments, using different primaries—orange, lime, purple, and teal—and obtained results similar to what occurred with red, green, blue, and yellow. That is, orange, lime, purple, and teal were rated as if they were "pure," so, for example, orange was rated as not containing any lime, purple, or teal (Bosten & Boehm, 2014).

What does this all mean? Opponent neurons are certainly important for color perception, because opponent responding is how color is represented in the cortex. But perhaps, as some researchers believe, the idea of unique hues may not be helping us figure out how neural responding results in specific colors. Apparently, it is not as simple as +M −L equals +G −R, which is directly related to perceiving green and red (Ocelak, 2015; Witzel et al., 2019).

If responses of +M −L neurons can't be linked to the perception of green and red, what is the function of these neurons? One idea is that opponent neurons indicate the *difference* in responding of pairs of cones. We can understand how this works at a neural level by looking at **Figure 9.26**, which shows how a +L −M neuron receiving excitation from the L-cone and inhibition from the M-cone responds to 500-nm and 600-nm lights. **Figure 9.26a** shows that the 500-nm light results in an inhibitory signal of −80 and an excitatory signal of +50, so the response of the +L −M neuron would be −30. **Figure 9.26b** shows that the 600-nm light results in an inhibitory signal of -25 and an excitatory signal of +75, so the response of the +L −M neuron would be +50. This "difference information" could be important in dealing with the large overlap in the spectra of the M and L cones.

Neurons with side-by-side receptive fields have also been used to provide evidence for a connection between color and form. These neurons can fire to oriented bars even when the intensity of the side-by-side bars is adjusted so they appear equally bright. In other words, these cells fire when the bar's form is determined only by differences in color. Evidence such as this has been used to support the idea of a close bridge between the processing of color and the processing of form in the cortex (Friedman et al., 2003; Johnson et al., 2008). Thus, when you look out at a colorful scene, the colors you see are not only "filling in" the objects and areas in the scene but may also be helping define the edges and shapes of these objects and areas.

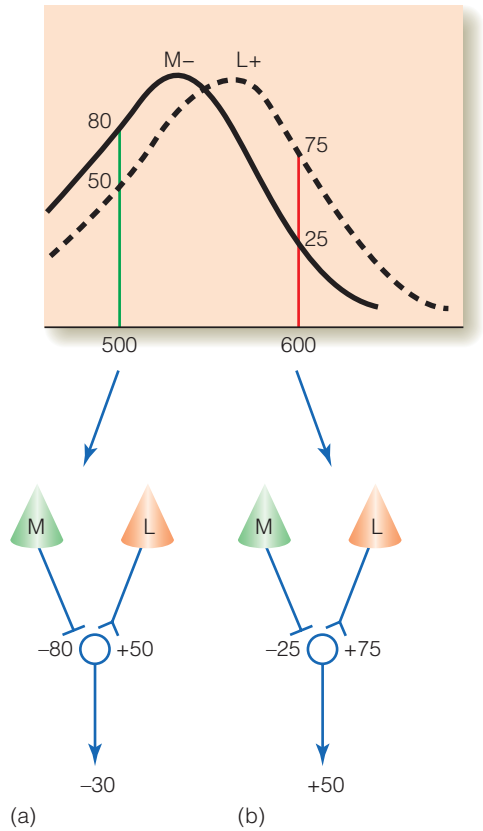

Figure 9.26 How opponent neurons determine the difference between the receptor responses to different wavelengths. (a) The response of the +L −M neuron to a 500-nm light is negative because the M receptor results in an inhibitory response that is larger than receptor L's excitatory response. This means the action of the 500-nm light on this neuron will cause a decrease in any ongoing activity. (b) The response to a 600-nm light is positive, so this wavelength causes an increase in the response of this neuron.

9.6 Color Areas in the Cortex

What are the cortical mechanisms of color perception? Is there one area in the cortex specialized for processing information about color? If there is such an area, that would make color similar to faces, bodies, and places, which can claim the fusiform face area (FFA), extrastriate body area (EBA), and parahippocampal place area (PPA) as specialized processing areas (see Chapter 5, page 110). The idea of an area specialized for color was popularized by Semir Zeki (1983a, 1983b, 1990) based on his finding that many neurons in a visual area called V4 respond to color.

However, additional evidence has led many researchers to reject the idea of a "color center" in favor of the idea that color processing is distributed across a number of cortical areas. The finding that there are a number of color-processing areas becomes even more interesting when the location of these areas is compared to areas associated with processing faces and places.

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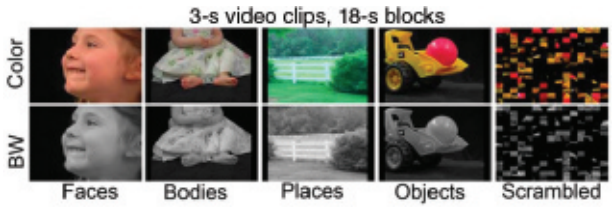

Figure 9.27 Images from 3-second video clips that were presented to participants in Lafer-Sousa and coworkers' (2016) experiment. The participants' brains were scanned as they watched the films. (Lafer-Sousa et al., 2016)

Rosa Lafer-Sousa and coworkers (2016) scanned participants' brains while they watched 3-second video clips that contained images like the ones shown in **Figure 9.27**. **Figure 9.28a** shows data from one hemisphere of a single individual. Notice that the color areas are sandwiched between areas that responded to faces and places. **Figure 9.28b** shows this "sandwiching" effect in a different view of the brain, which combines the results from a number of participants. Faces, color, and places are associated with different areas that are located next to each other.

The independence of shape and color is indicated by some cases of brain damage. Remember patient D.F. from Chapter 4, who could mail a card but couldn't orient the card or identify objects (Figure 4.26). She was described to illustrate a dissociation between action and object perception. But despite her difficulty in identifying objects, her color perception was unimpaired. Another patient, however, had the opposite problem with impaired color perception but normal form perception (Bouvier & Engle, 2006). This double dissociation means that color and form are processed independently (see Method: Double Dissociations in Neuropsychology, page 81).

But even though mechanisms for color, faces, and places are independent, the areas for faces and places are neighbors. That adjacency is likely what is behind the fact that 72 percent of patients with achromatopsia (color blindness), like Mr. I who we described at the beginning of the chapter, also have prosopagnosia—problems recognizing faces. So color processing in the cortex is both separate from other functions and closely related to them at the same time. This relationship may be behind the fact that color can play a role in perceptual organization (see page 97), attention (see page 130), and motion perception (Ramachandran, 1987).

We are left with lots of data showing how neurons respond to different wavelengths and how color is associated with numerous areas in the cortex, but we still don't know how signals from the three types of cones are transformed to cause our perception of color (Conway, 2009).

TEST YOURSELF 9.3

1. What did Hering's opponent-process theory propose?
2. What was Hering's phenomenological evidence for opponent-process theory?
3. Why wasn't Hering's theory widely accepted?
4. Describe Hurvich and Jameson's hue cancellation experiments. How was the result used to support opponent-process theory?
5. What is the physiological evidence for opponency?
6. What are unique hues?
7. Describe the modern hue scaling experiments that used colors other than red, green, blue, and yellow as the "primaries." What are the implications of these results?
8. Has it been possible to establish a connection between the firing of opponent neurons and our perception of specific colors?
9. What functions have been suggested for opponent neurons, in addition to their role in color perception?
10. Where is color represented in the cortex? How are the color areas related to areas for face and place processing?

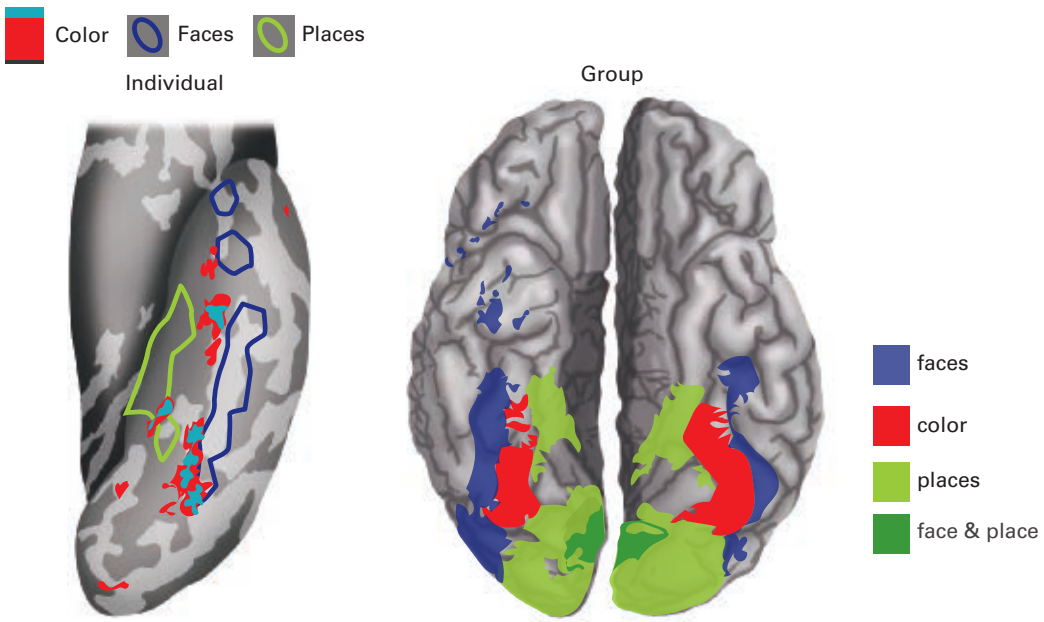

Figure 9.28 (a) Cortical areas that responded best to color (red and blue areas), faces (blue outline) and places (green outline) in one hemisphere of an individual (b) Areas for color (red), faces (blue), places (light green), and faces and places (dark green) determined from group data. (Lafer-Sousa et al., 2016)

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9.7 Color in the World: Beyond Wavelength

Throughout a normal day, we view objects under many different lighting conditions: morning sunlight, afternoon sunlight, indoors under incandescent light, indoors under fluorescent light, and so forth. So far in this chapter, we have only linked our perception of color to the light that is reflected from objects. What happens when the light shining on an object changes? In this section, we will think about the relationship between color perception and the light that is available in the environment.

Color Constancy

It is midday, with the sun high in the sky, and as you are walking to class you notice a classmate who is wearing a green sweater. Then, as you are sitting in class a few minutes later, you again notice the same green sweater. The fact that the sweater appears green both outdoors under sunlight illumination and indoors under artificial illumination may not seem particularly remarkable. After all, the sweater *is* green, isn't it? However, when we consider the interaction between illumination and the properties of the sweater, we can appreciate that your perception of the sweater as green, both outside and inside, represents a remarkable achievement of the visual system. This achievement is called **color constancy**—we perceive the colors of objects as being relatively constant even under changing illumination.

We can appreciate why color constancy is an impressive achievement by considering the interaction between illumination, such as sunlight or lightbulbs, and the reflection properties of an object, such as the green sweater. First, let's consider the illumination. **Figure 9.29a** shows the wavelengths of sunlight and the wavelengths emitted from incandescent (the "old style" tungsten bulbs that are being phased out) and newer light-emitting diode (LED) lightbulbs. Sunlight contains approximately equal amounts of energy at all wavelengths, which is a characteristic of white light. The incandescent bulb, however, contains much more energy at long wavelengths (which is why they look slightly yellow), whereas LED bulbs emit light at substantially shorter wavelengths (which is why they look slightly blue).

Now consider the interaction between the wavelengths produced by the illumination and the wavelengths reflected from the green sweater. The reflectance curve of the sweater is indicated in **Figure 9.29b**. It reflects mostly medium-wavelength light, as we would expect of something that is green.

The actual light that is reflected from the sweater depends both on its reflectance curve and on the illumination that reaches the sweater and is then reflected from it. To determine the wavelengths that are actually reflected from the sweater, we multiply the sweater's reflectance curve at each wavelength by the amount of illumination at each wavelength. The result of this calculation is shown in **Figure 9.29c**, which shows that light reflected from the sweater includes relatively more long-wavelength light when it is illuminated by incandescent light (the orange line in Figure 9.29c) than when it is illuminated by light from an LED bulb (the blue line in Figure 9.29c). The fact that we still see the sweater as green even though the wavelength composition of the reflected light differs under different illuminations is color constancy. Without color constancy, the color we see would depend on how the sweater was being illuminated (Delahunt & Brainard, 2004; Olkkonen et al., 2010).

Why does a green sweater look green even when viewed under different illuminations? The answer to this question involves a number of different mechanisms (Smithson, 2005). We begin by considering how the eye's sensitivity is affected by the color of the illumination of the overall scene, a process called *chromatic adaptation*.

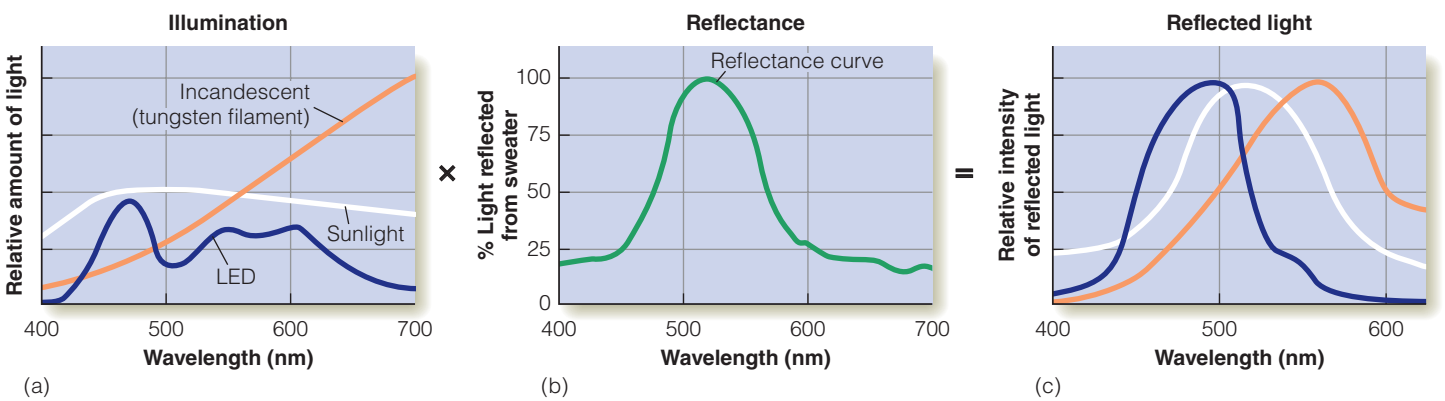

Figure 9.29 Determining what wavelengths are reflected from the green sweater under different illuminations. Light reflected from the sweater is determined by multiplying (a) the illumination of sunlight, incandescent, and LED lightbulbs times (b) the sweater's reflectance. The result is (c) the light reflected from the sweater. The maximum of each of the curves in (c) has been set at the same level to make the wavelength distributions easier to compare.

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Chromatic Adaptation The following demonstration highlights one factor that contributes to color constancy.

DEMONSTRATION | Adapting to Red

Illuminate **Figure 9.30** with a bright light from your desk lamp; then, with your left eye near the page and your right eye closed, look at the field with your left eye for about 30 to 45 seconds. Then look at various colored objects in your environment, blinking back and forth between your left eye and your right eye.

Figure 9.30 Red adapting field for "Adapting to Red" demonstration.

You may have noticed that adapting your left eye to the red decreased the redness of objects in the environment. This is an example of how color perception can be changed by chromatic adaptation—prolonged exposure to chromatic color. Adaptation to the red light selectively reduced the sensitivity of your long-wavelength cones, which decreased your sensitivity to red light and caused you to see the reds and oranges viewed with your left (adapted) eye as less saturated and bright than those viewed with the right eye.

The idea that chromatic adaptation is responsible for color constancy has been tested in an experiment by Keiji Uchikawa and coworkers (1989). Observers viewed isolated patches of colored paper under three different conditions (**Figure 9.31**): (a) *baseline*—paper and observer illuminated by white light; (b) *observer not adapted*—paper illuminated by red light, observer by white (the observer is not chromatically adapted); and (c) *observer adapted to red*—both paper and observer illuminated by red light (the observer is chromatically adapted).

The results from these three conditions are shown above each condition. In the *baseline* condition, a green paper is perceived as green. In the *observer not adapted* condition, the observer perceives the paper's color as being shifted toward the red. Color constancy does not occur in this condition because the observer is not adapted to the red light that is illuminating the paper. But in the *observer adapted to red* condition, perception is shifted only slightly to the red, so it appears more yellowish. Thus, the chromatic adaptation has created partial color constancy—the perception of the object is shifted after adaptation, but not as much as when there was no adaptation. This means that the eye can adjust its sensitivity to different wavelengths to keep color perception approximately constant as illumination changes.

This principle operates when you walk into a room illuminated with yellowish tungsten light. The eye adapts to the long-wavelength–rich light, which decreases your eye's sensitivity to long wavelengths. This decreased sensitivity causes the long-wavelength light reflected from objects to have less effect than before adaptation, and this compensates for the greater amount of long-wavelength tungsten light that is reflected from everything in the room. Because of this adaptation, the yellowish tungsten illumination has only a small effect on your perception of color.

A similar effect also occurs in environmental scenes, which can have different dominant colors in different seasons. For example, the same scene can be "lush" in summer, with a lot of green (**Figure 9.32a**) and "arid" in winter, with more yellows (**Figure 9.32b**). Based on calculations taking into account how this "greenness" and "yellowness" would affect the cone receptors, Michael Webster (2011) determined that adaptation to the green in the lush scene would decrease the perception of green in that scene (**Figure 9.32c**), and adaptation to the yellow of the arid scene would decrease the perception of yellow in the arid scene (**Figure 9.32d**). Thus, adaptation "tones down"

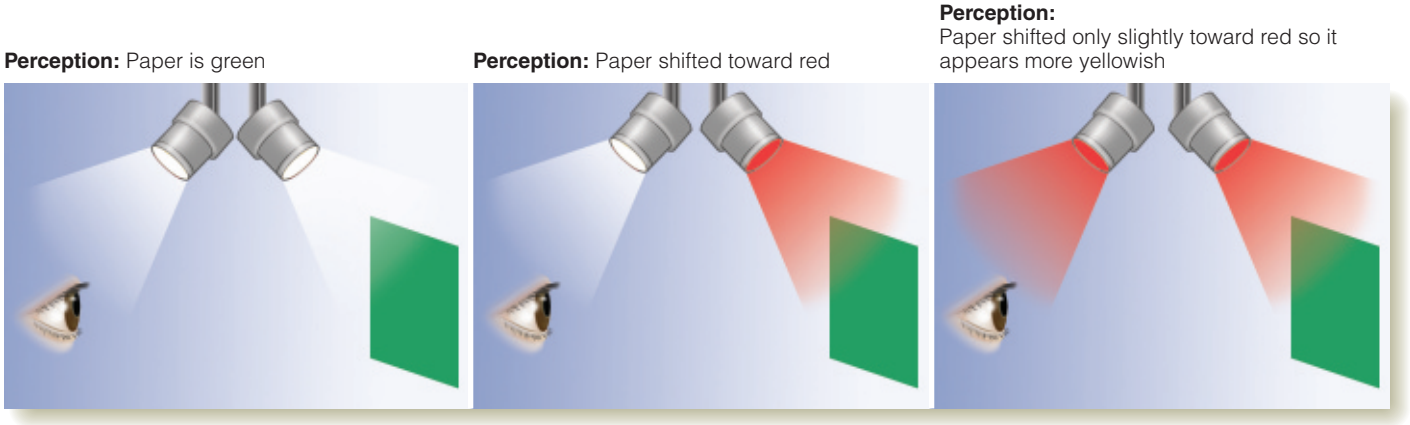
Perception: Paper is green
Perception: Paper shifted toward red
Perception:
Paper shifted only slightly toward red so it appears more yellowish
(a) Baseline
(b) Observer not adapted
(c) Observer adapted to red

Figure 9.31 The three conditions in Uchikawa and coworkers' (1989) experiment. See text for details.

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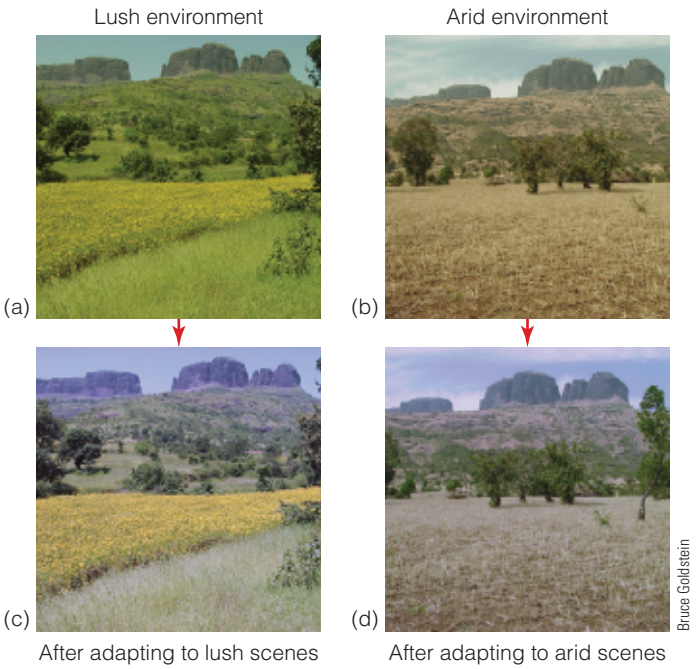

Figure 9.32 How chromatic adaptation to the dominant colors of the environment can influence perception of the colors of a scene. The dominant color of the scene in (a) is green. Looking at this scene causes adaptation to green and decreases the perception of green in the scene, as shown in (c). The dominant color of the arid scene in (b) is yellow. Adapting to this scene causes a decreased perception of yellow in the scene, as shown in (d). (Webster, 2011)

the dominant colors in a scene, so if we compare the *perceived* color of the lush and arid scenes in (c) and (d), we see that the colors are more similar than before the chromatic adaptation. This adaptation also causes novel colors to stand out, so yellow becomes more obvious in the lush scene and the green stands out in the arid scene.

Familiar Color Another thing that helps achieve color constancy is our knowledge about the usual colors of objects in the environment. This effect on perception of prior knowledge of the typical colors of objects is called **memory color**. Research has shown that because people know the colors of familiar objects, like a red stop sign or a green tree, they judge these familiar objects as having richer, more saturated colors than unfamiliar objects that reflect the same wavelengths (Ratner & McCarthy, 1990).

Thorsten Hansen and coworkers (2006) demonstrated an effect of memory color by presenting observers with pictures of fruits with characteristic colors, such as lemons, oranges, and bananas, against a gray background. Observers also viewed a spot of light against the same gray background. When the intensity and wavelength of the spot of light were adjusted so the spot was physically the same as the background, observers reported that the spot appeared the same gray as the background. But when the intensity and wavelength of the fruits were set to be physically the same as the background, observers reported that the fruits appeared slightly colored. For example, a banana that was physically the same as the gray background appeared slightly yellowish, and an orange looked slightly orange. This led Hansen to conclude that the observer's knowledge of the fruit's characteristic colors actually changed the colors they were experiencing. The effect of memory on our experience of color is a small one, but nonetheless may make a contribution to our ability to accurately perceive the colors of familiar objects under different illuminations.

Taking Illumination Into Account **Figure 9.33** shows two pictures of the same house taken under different illuminations at different times of day. The camera's color-correction mechanism has been turned off, so changes in illumination cause differences in color between the two pictures. The person who took these pictures reports, however, that the side of the house looked yellow both times (Brainard et al., 2006). While the camera disregarded the change in illumination, the human observer's visual system took it into account. One "taking into account" mechanism used by the visual system is chromatic adaptation, which we discussed earlier (Gupta et al., 2020).

But there are other mechanisms at work as well. A number of researchers have shown that color constancy works best when an object is surrounded by objects of many different colors, a situation that often occurs when viewing objects in the environment (Foster, 2011; Land, 1983, 1986; Land & McCann, 1971). It has also been shown that under some conditions, color constancy is better when objects are viewed with two eyes (which results in better depth perception) compared to one (Yang & Shevell, 2002), and that constancy is better when an object is observed in a three-dimensional scene, compared to when the observer looks at the scene through a kaleidoscope that scrambles the surrounding scene (Mizokami & Yagochi, 2014). Apparently, the surroundings and viewing conditions help us achieve color constancy because the visual system—in ways that are still not completely understood—uses the information in a scene to estimate the characteristics of

Figure 9.33 Photographs of a house taken at different times of day under different lighting conditions. Because the camera's color-correction mechanism is turned off, the change in illumination caused a change in the color of the siding from yellow to green. The photographer, however, reports that the siding looked yellow at both times of day. (Brainard et al., 2006)

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the illumination and to make appropriate corrections (Brainard, 1998, 2006; Mizokami, 2019; Smithson, 2005). The bottom line regarding color constancy is that even though it has been studied in hundreds of experiments, we still don't totally understand how the visual system takes the illumination into account. In the next section, we will consider another phenomenon that is related to color constancy and has proven difficult to explain.

#TheDress On February 26, 2015, a photograph of a striped dress similar to the one in **Figure 9.34** was posted online as #TheDress. What colors do you see in this photograph? The actual dress had alternating blue and black stripes (**Figure 9.35**). Many people saw it this way. But many other people saw the dress as alternating white and gold stripes, with a smaller group seeing black and white or other perceptions. The posting created a sensation. Why did people report seeing different colors when looking at the same picture?

Vision scientists quickly stepped into the discussion. The first step was to survey large groups of people to confirm the phenomenon. One survey reported that 57 percent of the people saw blue and black and 30 percent saw white and gold, with the other 13 percent perceiving other colors (Lafer-Sousa et al., 2015). Another survey reported quite different numbers:

Figure 9.34 An illustration of a striped dress similar to the one that has been perceived differently by different people. To see the original picture look up "The Dress" on Wikipedia.

Sarah Lee/eyevine/Redux

Figure 9.35 The Dress being held by Cecilia Bleasdale, who posted the picture on the Internet. This picture shows the black and blue stripes that are perceived when the dress is viewed "in person."

27 percent blue and black and 59 percent white and gold (Wallisch, 2017). But whatever the numbers, there was no question that blue–black and white–gold were the two predominant perceptions.

Given all the research that had been done in color vision before 2015, it would seem that vision researchers should be able to provide an explanation for these differing perceptions. However, that has not been the case. In the years following #TheDress, over a dozen papers appeared in scientific journals discussing how different people's perceptions could be influenced by differences between people such as the following: the wavelengths transmitted through the eye's optical system to the retina, the ratio of L to M cones, higher-order processing, people's language, how the picture is displayed on different devices, and interpretation of how the dress is illuminated. Although there is some evidence that differences in light transmission by the cornea and lens could make a small contribution to the effect (Rabin et al., 2016), the main explanations have suggested that differences in how people interpreted the illumination was responsible for the effect. And these explanations were based on the phenomenon of color constancy.

Here's how the color constancy explanation works: We've seen that perception of an object's color tends to remain

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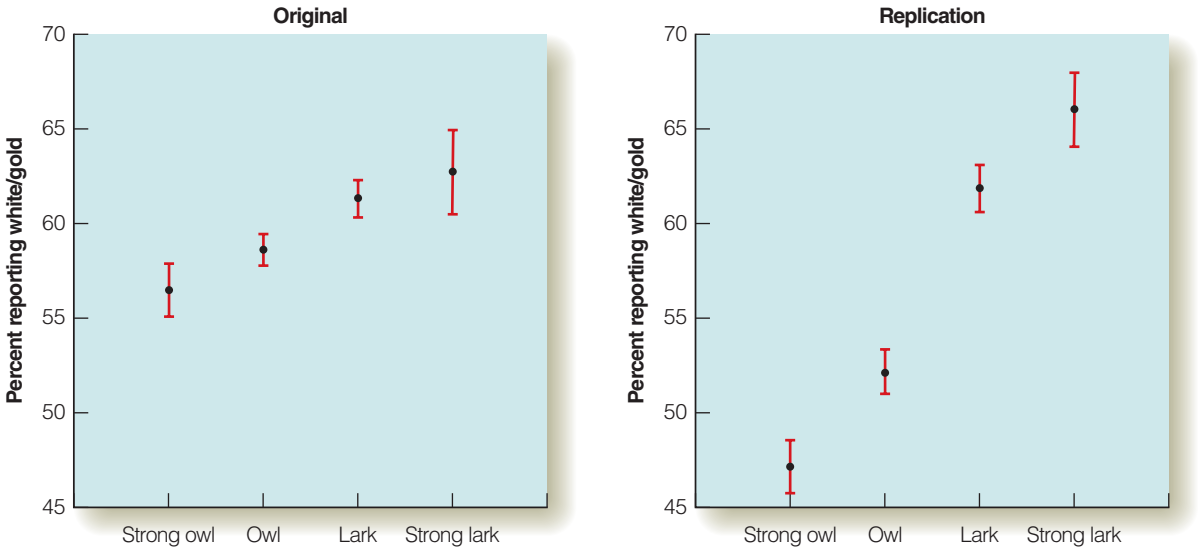

Figure 9.36 Percent of observers reporting the white–gold perception of The Dress photograph, as a function of being an "owl" (stays up late at night) or a "lark" (gets up early, goes to bed early). The two sets of data were obtained a year apart. Being a lark increases the chances of experiencing the white–gold perception. (Wallisch, 2017)

relatively constant even when the object is seen under different °illuminations. This occurs because the visual system takes the illumination into account and essentially "corrects" for changes in illumination so that the object's perception is based on the reflectance properties of the object's surface.

First, the actual dress is black and blue, as shown in Figure 9.35. So what would happen to perception of a black and blue dress if the illumination were rich in long wavelengths, like the "yellowish" light of old-style incandescent bulbs? The constancy mechanism will cause the visual system to decrease the effect of long wavelengths, so the blue will stay about the same, since blue objects usually reflect little long-wavelength light, and the black will get darker and perhaps a little bluer.

But what if a black and blue dress is assumed to be illuminated by "cooler" light, similar to daylight, which contains more short-wavelength "bluish" light? Discounting short wavelengths from the blue stripes would cause the blue stripes to be perceived as white and discounting short wavelengths from the black stripes would push perception of the black stripes toward yellow. If the reason for "black becoming yellow" isn't obvious, remember that a black object reflects a small amount of all wavelengths equally. Subtracting short wavelengths leaves the middle and long wavelengths associated with yellow light.

Some evidence consistent with this idea has been provided by Pascal Wallisch (2017), who reported the results of an online survey of over 13,000 people. The participants reported how they perceived the dress and also whether they classified themselves as "larks" (they get up early and go to bed early) or "owls" (they go to bed late and get up late). An important difference between larks and owls is that larks get more natural light, which contains more short wavelengths than owls, who stay up and are exposed to yellowish artificial incandescent light, which has a high content of long wavelengths.

Figure 9.36 shows the results of two surveys, taken a year apart, which shows that larks are more likely to see the dress as white–gold than owls. This result suggests that people's prior experience with illumination may affect the assumptions they are making about how the dress is being illuminated, with this assumption, in turn, affecting their perception of the colors of the dress. However, it is important to note that knowing someone is a lark or an owl doesn't do a very good job of predicting how they will see the dress. After all, in the second survey about 35 percent of larks saw the dress as blue–black and 47 percent of the owls saw it as white–gold.

Results such as those of Wallisch plus many other considerations have caused many vision researchers to suggest that the "corrective" mechanism of color constancy is the most likely explanation for The Dress, while acknowledging that we still don't totally understand the phenomenon. One thing is for sure: The Dress confirms something we knew already—our perception of color isn't determined solely by the wavelengths of light entering our eyes. Other things, including assumptions about the illumination, are at work.

The other thing the dress shows is that we still have a lot to learn about how color vision works. As color vision researchers David Brainard and Anya Hulbert (2015) stated in a paper published four months after the dress appeared, "A full understanding of the individual differences in how the dress is perceived will ultimately require data that relate on a person-by-person basis, the perception of the dress to a full set of individual difference measurements of colour vision." And Michael Webster (2018), in a comment published three years after the dress appeared, noted that "occasionally we are reminded of how little we know. ... The dress image ... made it obvious that our understanding of color is not at a point where explanations could come easily. In fact, very many aspects of color vision remain a mystery and the subject of intense activity, and new findings are constantly emerging that are challenging some of the most basic assumptions about color or are expanding the field in new directions."

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Interestingly, a similar phenomenon has recently been reported for speech, in which a sound recording created to indicate the correct pronunciation of "Laurel," has been perceived in two different ways when played back through a low-quality recorder. Some people hear "Laurel," but others hear "Yanny." Reacting to this result, Daniel Pressnitzer and coworkers (2018) exclaimed, "At long last, the world had the auditory equivalent of the visual sensation known as #TheDress." As we will discuss in Chapter 14, "Speech Perception," the explanation for Laurel/Yanny is different than the explanation for The Dress. However, one thing they have in common is that they both show that two people can perceive the same stimulus differently.

Lightness Constancy

Just as we perceive chromatic colors like red and green as remaining relatively constant even when the illumination changes, we also perceive achromatic colors—white, gray, and black—as remaining about the same when the illumination changes. Imagine, for example, a black Labrador retriever lying on a living room rug illuminated by a lightbulb. A small percentage of the light that hits the retriever's coat is reflected, and we see it as black. But when the retriever runs outside into the much brighter sunlight, its coat still appears black. Even though more light is reflected in the sunlight, the perception of the shade of achromatic color (white, gray, and black) remains the same. The fact that we see whites, grays, and blacks as staying about the same shade under different illuminations is called **lightness constancy**.

The visual system's problem is that the intensity of light reaching the eye from an object depends on two things: (1) the illumination—the *total amount of light* that is striking the object's surface—and (2) the object's **reflectance**—the *proportion of this light* that the object reflects into our eyes. When lightness constancy occurs, our perception of lightness is determined not by the *intensity of the illumination* hitting an object, but by the object's *reflectance*. Objects that look black reflect less than 10 percent of the light. Objects that look gray reflect about 10 to 70 percent of the light (depending on the shade of gray); and objects that look white, like the pages of a book, reflect 80 to 95 percent of the light. Thus, our perception of an object's lightness is related not to the *amount* of light that is reflected from the object, which can change depending on the illumination, but to the *percentage* of light reflected from the object, which remains the same no matter what the illumination.

You can appreciate the existence of lightness constancy by imagining a checkerboard, like the one in **Figure 9.37**, illuminated by room light. Let's assume that the white squares have a reflectance of 90 percent, and the black squares have a reflectance of 9 percent. If the illumination inside the room is 100 units, the white squares reflect 90 units and the black squares reflect 9 units (**Figure 9.37a**). Now, if we take the checkerboard outside into bright sunlight, where the illumination is 10,000 units, the white squares reflect 9,000 units of light and the black squares reflect 900 units (**Figure 9.37b**). But even though the black squares when outside reflect much more light than the white squares did when the checkerboard was inside, the black squares still look black. Your perception is determined by the reflectance, not the amount of light reflected. What is responsible for lightness constancy? There are a number of possible explanations.

The Ratio Principle

One observation about our perception of lightness is that when an object is illuminated evenly—that is, when the illumination is the same over the whole object, as in our checkerboard example—then lightness is determined by the *ratio* of reflectance of the object to the reflectance of surrounding objects. According to the **ratio principle**, as long as this ratio remains the same, the perceived lightness will remain the same (Jacobson & Gilchrist, 1988; Wallach, 1963). For example, consider one of the black squares in the checkerboard. The ratio of a black square to the surrounding white squares is 9/90 = 0.10 under low illuminations and 900/9,000 = 0.10 under high illuminations. Because the ratio of the reflectances is the same, our perception of the lightness remains the same.

The ratio principle works well for flat, evenly illuminated objects like our checkerboard. However, things get more complicated in three-dimensional scenes, which are usually illuminated unevenly.

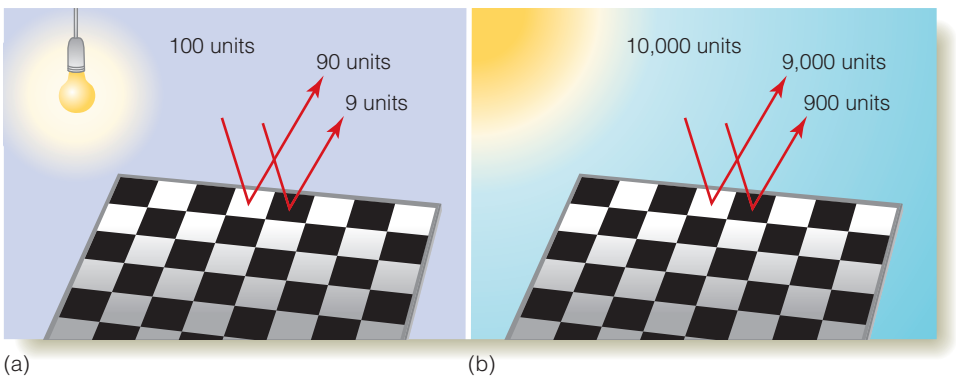

Figure 9.37 A black-and-white checkerboard illuminated by (a) tungsten light and (b) sunlight.

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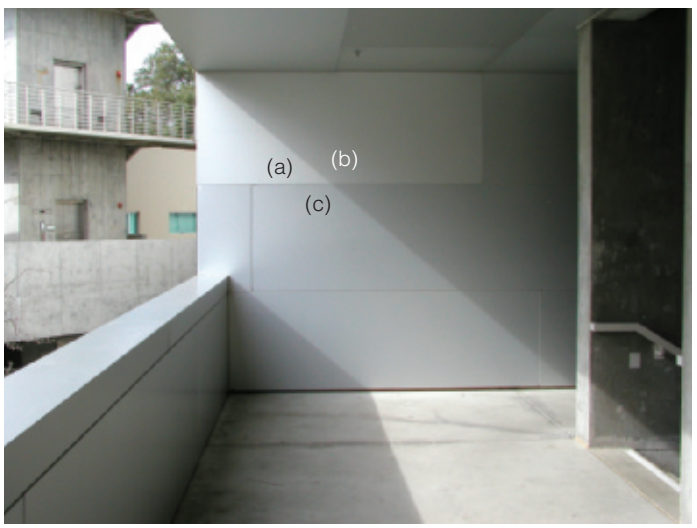
Lightness Perception Under Uneven Illumination If you look around, you will probably notice that the illumination is not even over the entire scene, as was the case for our two-dimensional checkerboard. The illumination in three-dimensional scenes is usually uneven because of shadows cast by one object onto another or because one part of an object faces the light and another part faces away from the light. For example, in **Figure 9.38**, in which a shadow is cast across a wall, we need to determine whether the changes in appearance we see across the wall are due to differences in the properties of different parts of the wall or to differences in the way the wall is illuminated.

The problem for the perceptual system is that it has to somehow take the uneven illumination into account. One way to state this problem is that the perceptual system needs to distinguish between *reflectance edges* and *illumination edges*. A **reflectance edge** is an edge where the reflectance of two surfaces changes. The border between areas *a* and *c* in Figure 9.38 is a reflectance edge because the two surfaces are made of different materials that reflect different amounts of light. An **illumination edge** is an edge where the lighting changes. The border between *a* and *b* is an illumination edge because area *a* is receiving more light than area *b*, which is in shadow.

Some explanations for how the visual system distinguishes between these two types of edges have been proposed (see Adelson, 1999; Gilchrist, 1994; and Gilchrist et al., 1999, for details). The basic idea behind these explanations is that the perceptual system uses a number of sources of information to take illumination into account.

The Information in Shadows In order for lightness constancy to work, the visual system needs to be able to take the uneven illumination created by shadows into account. It must determine that this change in illumination caused by a shadow is due to an illumination edge and not to a reflectance edge. Obviously, the visual system usually succeeds in doing this because although the light intensity is reduced by shadows, you don't usually see shadowed areas as gray or black. For example, in the case of the wall in **Figure 9.39**, the shadowed area looks different than the sunny area, but you know it's a shadow so you infer that the color of the bricks in the shadowed area is actually the same as the color in the sunny area. In other words, you are taking into account the fact that less light is falling on the shadowed area.

How does the visual system know that the change in intensity caused by the shadow is an illumination edge and not a reflectance edge? One thing the visual system may take into account is the shadow's meaningful shape. In this particular example, we know that the shadow was cast by a tree, so we know it is the illumination that is changing, not the color of the bricks on the wall. Another clue is provided by the nature of the shadow's contour, as illustrated by the following demonstration.



Bruce Goldstein

Figure 9.38 This unevenly illuminated wall contains both reflectance edges (between *a* and *c*) and illumination edges (between *a* and *b*). The perceptual system must distinguish between these two types of edges to accurately perceive the actual properties of the wall, and other parts of the scene as well.

Bruce Goldstein

Figure 9.39 In this photo, you assume that the shadowed and unshadowed areas are bricks with the same lightness but that less light falls on some areas than on others because of the shadow cast by the tree.

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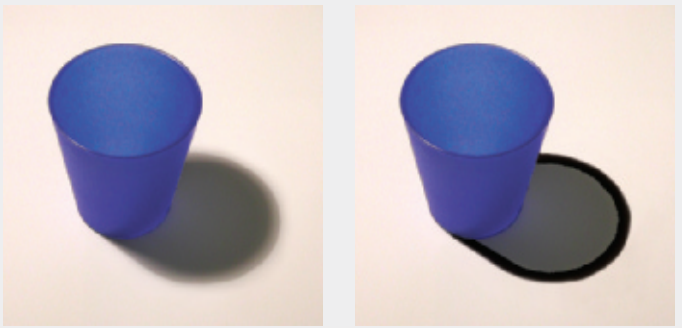
DEMONSTRATION | The Penumbra and Lightness Perception

Place an object, such as a cup, on a white piece of paper on your desk. Then illuminate the cup at an angle with your desk lamp and adjust the lamp's position to produce a shadow with a slightly fuzzy border, as in **Figure 9.40a**. (Generally, moving the lamp closer to the cup makes the border get fuzzier.) The fuzzy border at the edge of the shadow is called the shadow's penumbra. Now take a marker and draw a thick line, as shown in **Figure 9.40b**, so you can no longer see the penumbra. What happens to your perception of the shadowed area inside the black line?



Bruce Goldstein

(a) (b)

Figure 9.40 (a) A cup and its shadow. (b) The same cup and shadow with the penumbra covered by a black border.

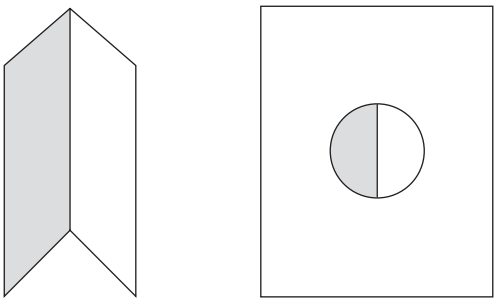
Covering the penumbra causes most people to perceive a change in the appearance of the shadowed area. Apparently, the penumbra provides information to the visual system that the dark area next to the cup is a shadow, so the edge between the shadow and the paper is an illumination edge. However, masking off the penumbra eliminates that information, so the area covered by the shadow is seen as a change in reflectance. In this demonstration, lightness constancy occurs when the penumbra is present but does not occur when it is masked.

The Orientation of Surfaces The following demonstration provides an example of how information about the orientation of a surface affects our perception of lightness.

DEMONSTRATION | Perceiving Lightness at a Corner

Stand a folded index card on end so that it resembles the outside corner of a room, and illuminate it so that one side is illuminated and the other is in shadow. When you look at the corner, you can easily tell that both sides of the corner are made of the same white material but that the nonilluminated side is shadowed (**Figure 9.41a**). In other words, you perceive the edge between the illuminated and shadowed "walls" as an illumination edge.

Now create a hole in another card and, with the hole a few inches from the corner of the folded card, view the corner with one eye about a foot from the hole (**Figure 9.41b**). If, when viewing the corner through the hole, you perceive the corner as a flat surface, your perception of the left and right surfaces will change.



(a) (b)

Figure 9.41 Viewing a shaded corner. (a) Illuminate the card so one side is illuminated and the other is in shadow. (b) View the card through a small hole so the two sides of the corner are visible, as shown.

In this demonstration, the illumination edge you perceived at first became transformed into an erroneous perception of a reflectance edge, so you saw the shadowed white paper as being gray paper. The erroneous perception occurs because viewing the shaded corner through a small hole eliminated information about the conditions of illumination and the orientation of the corner. In order for lightness constancy to occur, it is important that the visual system have adequate information about the conditions of illumination. Without this information, lightness constancy can break down and a shadow can be seen as a darkly pigmented area.

Figure 9.42a provides another example of a possible confusion between perceiving an area as being "in shadow" or perceiving it as being made of "dark material." This photograph of the statue of St. Mary was taken at night in the Grotto of Our Lady of Lourdes at the University of Notre Dame. As I (BG) observed the statue at night, it was unclear to me whether the dark area above Mary's arms was colored blue, like the sash, or whether it was simply in shadow. I suspected the shadow explanation, but the almost perfect color match between that area and the sash made me wonder whether the area about Mary's arms were, in fact, blue. The statue is perched on a high ledge, so it wasn't easy to tell, so I returned the next morning to see Mary in daylight. **Figure 9.42b** reveals that the dark area was, in fact, a shadow. Mystery solved! As with color perception, sometimes we are fooled by conditions of illumination or by ambiguous information, but most of the time we perceive lightness accurately.

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Bruce Goldstein

Figure 9.42 (a) A statue of St. Mary illuminated at night from below. (b) The same statue during the day.

SOMETHING TO CONSIDER:

We Perceive Color From Colorless Wavelengths

Our discussion so far has been dominated by the idea that there is a connection between wavelength and color. This idea is most strongly demonstrated by the visual spectrum in which each wavelength is associated with a specific color (**Figure 9.43a**). But this connection between wavelength and color can be misleading, because it might lead you to believe that wavelengths are colored—450-nm light is blue, 520-nm light is green, and so on. As it turns out, however, wavelengths are completely colorless. This is demonstrated by considering what happens to our perception of color under dim illumination, as happens at dusk. As illumination decreases, we dark adapt and our vision shifts to the rods (pp. 46, 54). This causes hues such as blue, green, and red to become less distinct and eventually disappear altogether, until the spectrum, once lushly colored, becomes a series of different shades of gray (**Figure 9.43b**). This effect of dark adaptation illustrates that the nervous system constructs color from wavelengths through the action of the cones.

The idea that color is *not* a property of wavelengths was asserted by Isaac Newton in his *Optiks* (1704):

> The Rays to speak properly are not coloured. In them there is nothing else than a certain Power and Disposition to stir up a Sensation of this or that

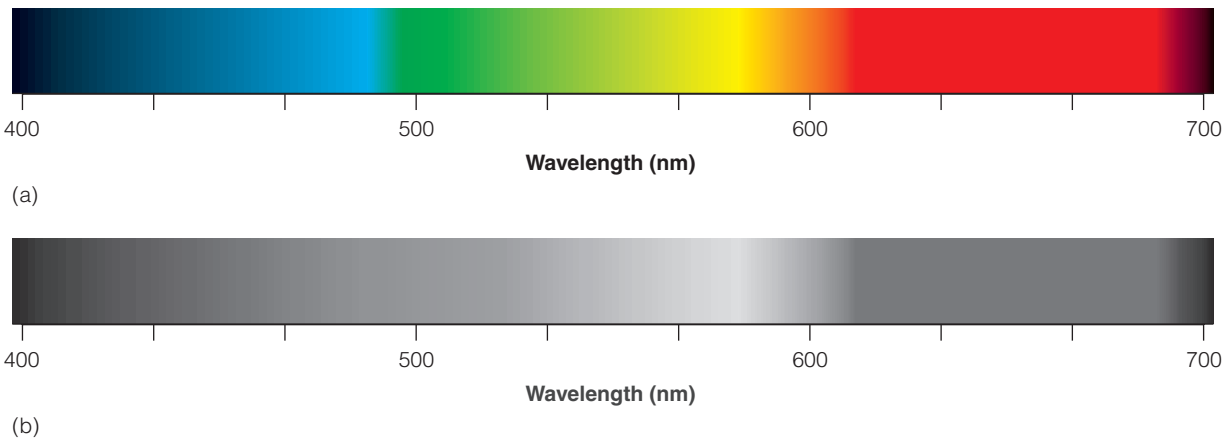

Figure 9.43 (a) Visible spectrum in color. (b) Spectrum as perceived at low intensities, when only the rod receptors are controlling vision.

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> Colour. ... So Colours in the Object are nothing but a Disposition to reflect this or that sort of Rays more copiously than the rest.

Newton's idea is that the colors we see in response to different wavelengths are not contained in the rays of light themselves, but that the rays "stir up a sensation of this or that color." Stating this idea in modern-day physiological terms, we would say that light rays are simply energy, so there is nothing intrinsically "blue" about short wavelengths or "red" about long wavelengths, and that we perceive color because of the way our nervous system responds to this energy.

We can appreciate the role of the nervous system in creating color experience by considering not only what happens when vision shifts from cone to rod receptors but also the fact that people like Mr. I., the artist who lost his ability to see color in a car accident, see no colors, even though they are receiving the same stimuli as people with normal color vision. Also, many animals perceive either no color or a greatly reduced palette of colors compared to humans, and others sense a wider range of colors than humans, depending on the nature of their visual systems.

For example, **Figure 9.44** shows the absorption spectra of a honeybee's visual pigments. The pigment that absorbs short-wavelength light enables the honeybee to see short wavelengths that can't be detected by humans (Menzel & Backhaus, 1989; Menzel et al., 1986). What "color" do you think bees perceive at 350 nm, which you can't see? You might be tempted to say "blue" because humans see blue at the short-wavelength end of the spectrum, but you really have no way of knowing what the honeybee is seeing, because, as Newton stated, "The Rays ... are not coloured." There is no color in the wavelengths; it is the bee's nervous system that creates the bee's experience of color. For all we know, the honeybee's experience of color at short wavelengths is quite different from ours, and may also be different for wavelengths in the middle of the spectrum that humans and honeybees can both see.

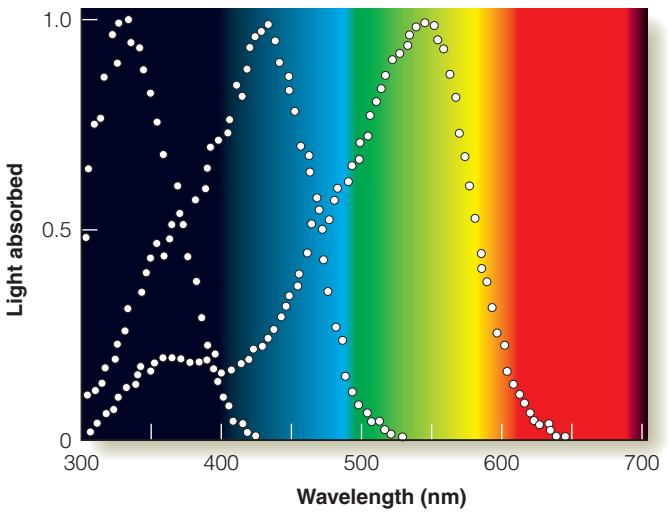
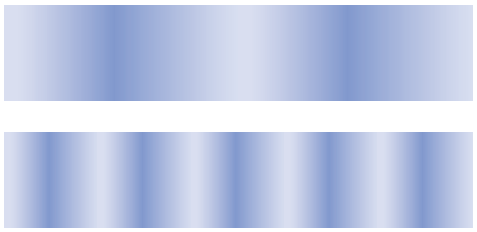


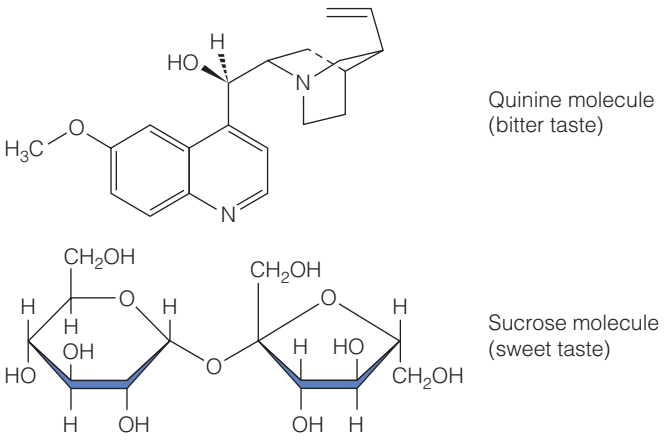
Figure 9.44 Absorption spectra of honeybee visual pigments.

The idea that the nervous system is responsible for the quality of our experience also holds for other senses. For example, we will see in Chapter 11 that our experience of hearing is caused by pressure changes in the air. But why do we perceive slow pressure changes as low pitches (like the sound of a tuba) and rapid pressure changes as high pitches (like a piccolo)? Is there anything intrinsically "high-pitched" about rapid pressure changes (**Figure 9.45a**)? Or consider the sense of taste. We perceive some substances as "bitter" and others as "sweet," but where is the "bitterness" or "sweetness" in the molecular structure of the substances that enter the mouth? Again, the answer is that these perceptions are not in the molecular structures. They are created by the action of the molecular structures on the nervous system (**Figure 9.45b**).

One of the themes of this book has been that our experience is created by our nervous system, so the properties of the nervous system can affect what we experience. We know, for example, that our ability to detect dim lights and fine details is affected by the way the rod and cone receptors converge onto other neurons in the retina (see Chapter 3, pages 53, 54). The idea we have introduced here is that our perceptual experience is not only *shaped* by the nervous system, as in the example of rod and cone vision, but—in cases such as color vision, hearing, taste, and smell—the very essence of our experience is *created* by the nervous system.



(a) Where are the high and low pitches?



(b) Where are the bitter and sweet tastes?

Figure 9.45 (a) Low and high pitches are associated with slow and fast pressure waves, but pressure waves don't have "pitch." The pitch is created by how the auditory system responds to the pressure waves. (b) Molecules don't have taste. The nervous system creates different tastes in response to the action of the molecules on the taste system.

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We know that our perception of color is determined by the action of three different types of cone receptors (Figure 9.13). Because the cones are poorly developed at birth, we can guess that the newborn would not have good color vision. However, research has shown that color vision develops early and that appreciable color vision is present within the first 3 to 4 months of life.

In a classic early experiment, Marc Bornstein and coworkers (1976) assessed the color vision of 4-month-old infants by determining whether they perceived the same color categories in the spectrum as adults. People with normal trichromatic vision see the spectrum as a sequence of color categories, starting with blue at the short-wavelength end, followed by green, yellow, orange, and red, with fairly abrupt transitions between one color and the next (see the spectrum in Figure 9.4b).

Bornstein used the **habituation procedure** to determine whether infants perceived color categories by presenting a 510-nm light—a wavelength that appears green to an adult with normal color vision (see Figure 9.44)—a number of times and measuring how long the infant looked at it (**Figure 9.46**). The decrease in looking time (green dots) indicates that habituation occurs as the infant becomes more familiar with the color.

The moment of truth in the habituation procedure is based on the fact that infants like looking at novel stimuli. So presenting a different light will catch the infant's attention if the infant perceives it as different. This is what happens when a 480-nm light is presented on trial 16. This light appears blue to an adult observer and is therefore in a different category than the 510-nm light, and the infants' increase in looking time, called **dishabituation**, indicates that the infant also perceived the 480-nm light as different than 510-nm light, and is therefore in a different category. However, when this procedure is repeated, first habituating to a 510-nm light and then presenting a 540-nm light (which is also perceived as green by adults and so is in the same category), dishabituation does not occur, indicating that the 540-nm light is in the same category as the 510-nm light for the infants. From this result and the results of other experiments, Bornstein concluded that 4-month-old infants categorize colors the same way adult trichromats do.

A more recent experiment used another procedure, called the **novelty-preference procedure**, to study infant color vision. Anna Franklin and Ian Davies (2004) had 4- to 6-month-old infants look at a display like the one in **Figure 9.47a**, in which two side-by-side squares had the same color. In this *familiarization* part of the experiment, the infants habituated—their looking time to the colored areas decreased—as the stimulus was repeatedly presented. In the *novelty preference* part of the experiment, a new color was presented in one of the squares, as in **Figure 9.47b**, and the infants' looking patterns were again measured.

To determine whether infants saw different colors across category boundaries, the infants were shown two types of pairs in the novelty test. For the "within pairs" condition, the new

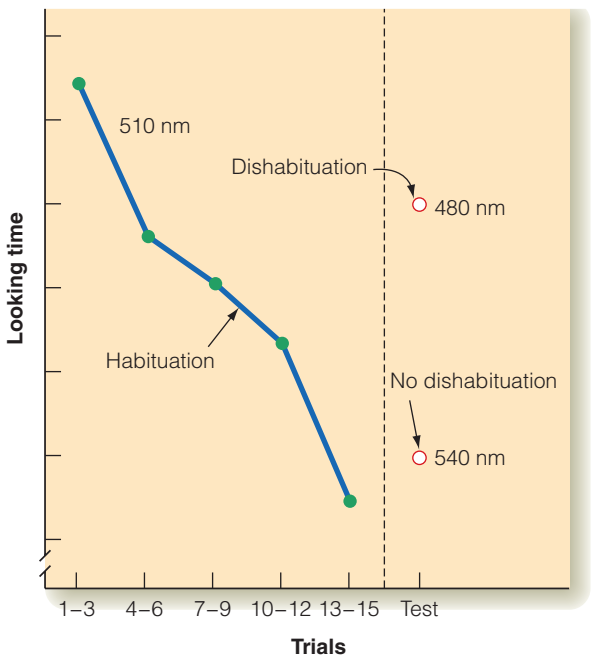

Figure 9.46 Results of the Bornstein et al. (1976) experiment. Looking time decreases over the first 15 trials as the infant habituates to repeated presentations of a 510-nm stimulus. Looking times for presentation of 480-nm and 540-nm stimuli presented on trial 16 are indicated by the dots on the right.

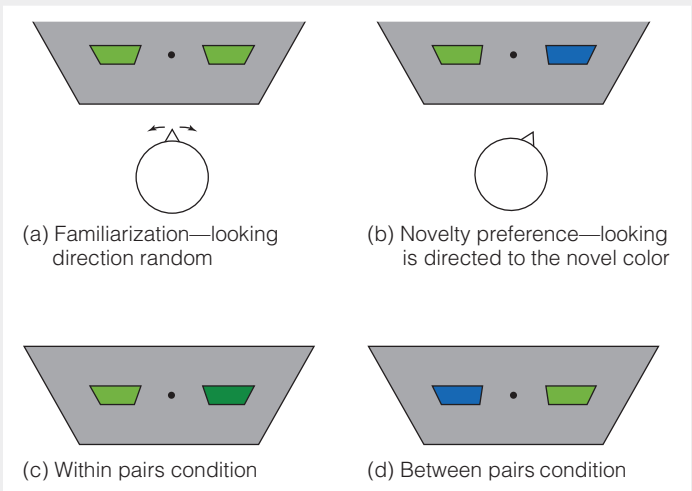
(a) Familiarization—looking direction random
(b) Novelty preference—looking is directed to the novel color
(c) Within pairs condition
(d) Between pairs condition

Figure 9.47 In Franklin and Davies' (2004) experiment, the looking times of 4- to 6-month-old infants are measured during (a) the "familiarization" part of the experiment in which the two squares are identical, (b) the "novelty preference" part of the experiment, in which one of the squares is changed, (c) the "within pairs" condition, in which the two squares are in the same color category, and (d) the "between pairs" condition, in which the squares are in different categories.

Continued

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color was within an adult category, as in **Figure 9.47c**, both of which are in the "green" category. For the "between pairs" condition, the new color was in a different adult category, as in **Figure 9.47d**, where the new color is blue. Franklin and Davies found that when the colors in the two squares were both within the same adult category, the infants' looking times were equally distributed between the two squares. However, if the colors were in different adult categories, infants looked at the newly presented color about 70 percent of the time.

Franklin and Davies got the same result for other pairs of colors (red–pink and blue–purple) and concluded that "4-month-old infants seem to have adult perceptual color categories, at least to some degree." In another experiment, which compared more colors in 6-month-old infants, Alice Skelton and coworkers (2017) concluded that the infants distinguished blue, green, purple, yellow, and red categories.

What's particularly significant about these results is that infants achieve this categorization of color before they have acquired language. This has led researchers to conclude that sorting colors into categories depends not on higher-level processes like language, but is determined by early mechanisms based on the cone receptors and how they are wired-up (Maule and Franklin, 2019).

As with all research in which we are drawing conclusions about how things appear to people, it is important to realize that research that indicates that infants categorize colors in the same way as adults doesn't tell us how those colors *appear* to the infants (Dannemiller, 2009). Just as it is not possible to know whether two adults who call a light "red" are having exactly the same experience, it is also not possible to know exactly what the infants are experiencing when their looking behavior indicates that they can tell the difference between two colors. In addition, there is evidence that color vision continues to develop into the teenage years (Teller, 1997). It is safe to say, however, that the foundations of trichromatic vision are present at about 4 months of age.

TEST YOURSELF 9.4

1. What is color constancy? What would our perceptual world be like without color constancy?
2. Describe chromatic adaptation. How is it demonstrated by Uchikawa's experiment?
3. How does color constancy work when walking into a room illuminated by a tungsten light? When the seasons change?
4. What is the evidence that memory can have a small effect on color perception?
5. Describe the mechanisms that help achieve color constancy by taking illumination into account.
6. What does it mean to say that the surroundings help achieve color constancy?
7. What is #TheDress? What explanations have been proposed to explain this phenomenon?
8. What is lightness constancy? Describe the roles of illumination and reflectance in determining perceived lightness.
9. How is the ratio principle related to lightness constancy?
10. Why is uneven illumination a problem for the visual system? What are the two types of edges that are associated with uneven illumination?
11. How is lightness perception affected by shadows? What cue for shadows occurs at the shadow's border?
12. Describe the "folded card" demonstration. What does it show about how lightness is affected by our perception of the orientation of surfaces?
13. What does it mean to say that color is created by the nervous system?
14. Describe the habituation procedure and the novelty-preference procedure for determining how infants categorize color. What conclusion was reached from these experiments? What do the results of these experiments tell us about what the infants are experiencing?

THINK ABOUT IT

1. A person with normal color vision is called a trichromat. This person needs to mix three wavelengths to match all other wavelengths and has three cone pigments. A person who is color deficient is called a dichromat. This person needs only two wavelengths to match all other wavelengths and has only two operational cone pigments. A tetrachromat needs four wavelengths to match all other wavelengths and has four cone pigments. If a tetrachromat were to meet a trichromat, would the tetrachromat think that the trichromat was color deficient? How would the tetrachromat's color vision be "better than" the trichromat's? (p. 208)
2. When we discussed color deficiency, we noted the difficulty in determining the nature of a color-deficient person's color experience. Discuss how this is related to the idea that color experience is a creation of our nervous system. (p. 223)
3. When you walk from outdoors, which is illuminated by sunlight, to an indoor space that is illuminated by

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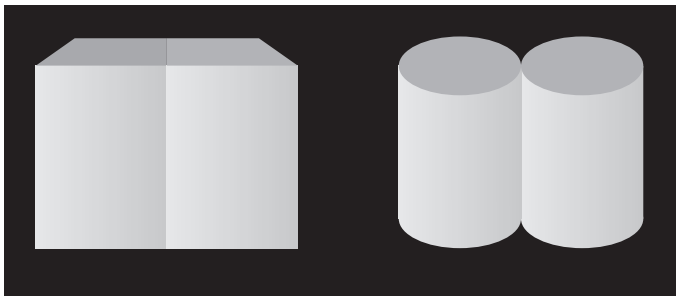
tungsten or LED bulbs, your perception of colors remains fairly constant. But under some illuminations, such as sodium-vapor lights that sometimes illuminate highways or parking lots, colors do seem to change. Why do you think color constancy would hold under some illuminations but not others? (p. 215)

4. **Figure 9.48** shows two displays (Knill & Kersten, 1991). The display in (b) was created by changing the top and bottom of the display in (a), while keeping the intensity distributions across the centers of the displays constant. (You can convince yourself that this is true by masking off the top and bottom of the displays.) But even though the intensities are the same, the display in (a) looks like a dark surface on the left and a light surface on the right, whereas the display in (b) looks like two curved cylinders with a slight shadow on the left one. How would you explain this, based on what we know about the causes of lightness constancy? (p. 220)



(a) (b)

Figure 9.48 The light distribution is identical for (a) and (b), although it appears to be different. (Figure courtesy of David Knill and Daniel Kersten)

KEY TERMS

#TheDress (p. 218)
Aberration (p. 205)
Achromatic colors (p. 200)
Adaptive optical imaging (p. 205)
Additive color mixture (p. 202)
Anomalous trichromatism (p. 210)
Cerebral achromatopsia (p. 197)
Chromatic adaptation (p. 216)
Chromatic colors (p. 200)
Color blind (p. 207)
Color circle (p. 210)
Color constancy (p. 215)
Color deficiency (p. 198)
Color matching (p. 205)
Color solid (p. 203)
Cone mosaic (p. 206)
Desaturated (p. 203)
Deuteranopia (p. 209)
Dichromat (p. 208)
Dichromatism (p. 209)
Dishabituation (p. 225)
Habituation procedure (p. 225)
Hue (p. 203)
Hue cancellation (p. 211)
Hue scaling (p. 211)
Illumination edge (p. 221)
Ishihara plate (p. 208)
Lightness constancy (p. 220)
Memory color (p. 217)
Metamerism (p. 206)
Metamers (p. 206)
Microspectrophotometry (p. 205)
Monochromat (p. 207)
Monochromatism (p. 207)
Munsell color system (p. 203)
Neutral point (p. 209)
Nonspectral colors (p. 203)
Novelty-preference procedure (p. 225)
Opponent neurons (p. 211)
Opponent-process theory of color vision (p. 210)
Partial color constancy (p. 216)
Penumbra (p. 222)
Primary colors (p. 211)
Principle of univariance (p. 207)
Protanopia (p. 209)
Ratio principle (p. 220)
Reflectance (p. 220)
Reflectance curves (p. 200)
Reflectance edge (p. 221)
Saturation (p. 203)
Selective reflection (p. 200)
Selective transmission (p. 200)
Spectral colors (p. 203)
Subtractive color mixture (p. 202)
Transmission curves (p. 200)
Trichromacy of color vision (p. 204)
Trichromat (p. 208)
Tritanopia (p. 209)
Unilateral dichromat (p. 209)
Unique hues (p. 211)
Value (p. 203)
Young-Helmholtz theory (p. 204)

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Looking out over this scene, we are able to perceive the distances of objects ranging from very close to far into the distance. We are also able to make judgments about the sizes of objects, and although the church steeple is smaller in our field of view than the nearby structure on the right, we know that the church is much larger. Our perception of depth and size are closely related.

Bruce Goldstein

Learning Objectives

After studying this chapter, you will be able to …

- Describe the basic problem involved in perceiving depth based on the two-dimensional information on the retina.
- Describe the different monocular (one-eyed) cues for depth.
- Understand how the two eyes cooperate to create binocular (two-eyed) cues for depth.
- Describe how neural signals coming from the two eyes are combined to create depth perception.
- Understand how animals ranging from monkeys, to cats, to pigeons, to insects perceive depth.
- Understand how perceiving an object's size depends on being able to perceive how far away it is.
- Describe how the connection between the perception of size and depth has been used to explain size illusions.
- Describe procedures that have been used to determine the types of information young infants use to perceive depth.

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CHAPTER 10

Perceiving Depth and Size

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DEVELOPMENTAL DIMENSION: Infant Depth Perception

Binocular Disparity

Pictorial Cues

METHOD: Preferential Reaching

TEST YOURSELF 10.2

THINK ABOUT IT

Some Questions We Will Consider:

- How can we see far into the distance based on the two-dimensional image on the retina? (pp. 231, 236)
- Why do we see depth better with two eyes than with one eye? (p. 236)
- Why don't people appear to shrink in size when they walk away? (p. 250)

Our final chapter on vision focuses on the perception of depth and size. At first, you might think that depth and size are separate issues in perception, but they are in fact closely related. To see why, let's consider **Figure 10.1a**. What do you see in this image? Most people see what appears to be a very small man standing on a chair. This is, however, an illusion created by a misperception of the man's distance from the camera. Although the man appears to be standing on a chair that is next to the woman, he is actually standing on a platform located next to the black curtain (**Figure 10.1b**). The illusion that the man is standing on a chair is created by lining up the camera so a structure located across from the woman lines up with the platform, to create the perception of a chair. Showing the woman apparently pouring into the man's glass enhances the misperception of the man's distance, and our incorrect perception of his depth leads to an incorrect perception of his size.

The illusion in Figure 10.1 was specifically created to trick your brain into misperceiving the man's depth and size, but why don't we confuse a small man who is close by and a large man who is far away in our everyday perception of the world? We will answer this question by describing the many ways we use different sources of optical and environmental information to help us determine the depth and size of objects in our everyday environments.

10.1 Perceiving Depth

You can easily tell that the page or screen text you are reading is about 12 to 18 inches away and, when you look up at the scene around you, that other objects are located at

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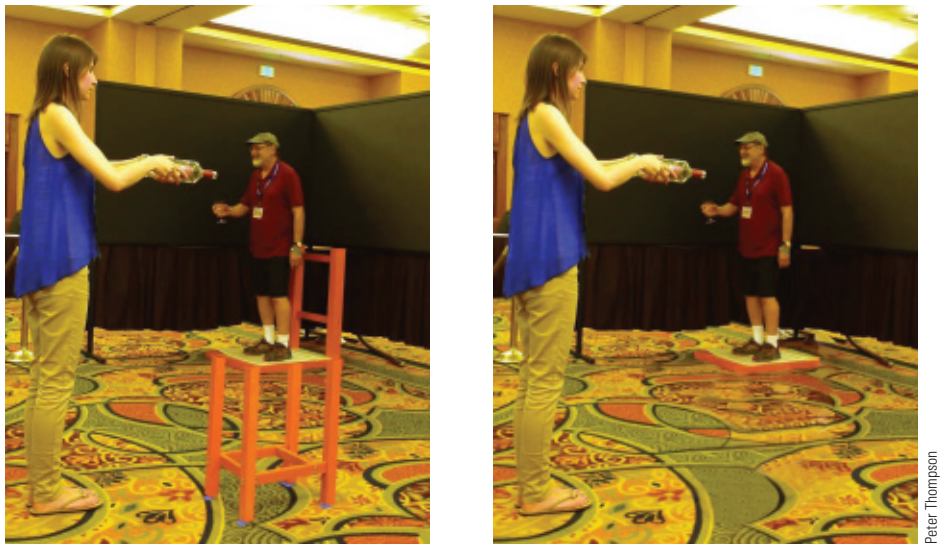

Figure 10.1 (a) Misperception of the man's depth leads to an incorrect perception of his size. (b) When the illusion of the "chair" is removed, the man's actual depth can be determined, and he appears to be of normal height.

distances ranging from your nose (very close!) to across the room, down the street, or even as far as the horizon, depending on where you are. What's amazing about this ability to see the distances of objects in a three-dimensional environment is that your perception of these objects, and the scene as a whole, is based on the two-dimensional image on your retina.

We can appreciate the problem of perceiving three-dimensional depth based on the two-dimensional information on the retina by considering two points on the scene in **Figure 10.2a**. Light is reflected from point T on the tree and from point H on the house onto points T′ and H′ on the retina at the back of the eye. Looking just at these points on the flat surface of the retina (**Figure 10.2b**), we have no way of knowing how far the light has traveled to reach each point. For all we know, the light stimulating either point on the retina could have come from 1 foot away or from a distant star. Clearly, we need to expand our view beyond single points on the retina to determine where objects are located in space.

When we expand our view from two isolated points to the entire retinal image, we increase the amount of information available to us because now we can see the images of the house and the tree. However, because this image is two-dimensional, we still need to explain how we get from the flat image on the retina to the three-dimensional perception of the scene.

One way researchers have approached this problem is by the **cue approach to depth perception**, which focuses on identifying information in the retinal image that is correlated with depth in the scene. For example, when one object partially covers another object, as the tree in the foreground in Figure 10.2a covers part of the house, the object that is partially covered must be farther than the object that is covering it. This situation, called **occlusion**, is a cue that one object is in front of another. According to cue theory, we learn the connection between this cue and depth through our previous experience with the environment. After this learning has occurred, the association between particular cues and depth becomes automatic, and when these depth cues are present, we experience the world in three dimensions. A number of different types of cues that signal depth in a scene have been identified. We can divide these cues into three major groups:

1. *Oculomotor.* Cues based on our ability to sense the position of our eyes and the tension in our eye muscles.

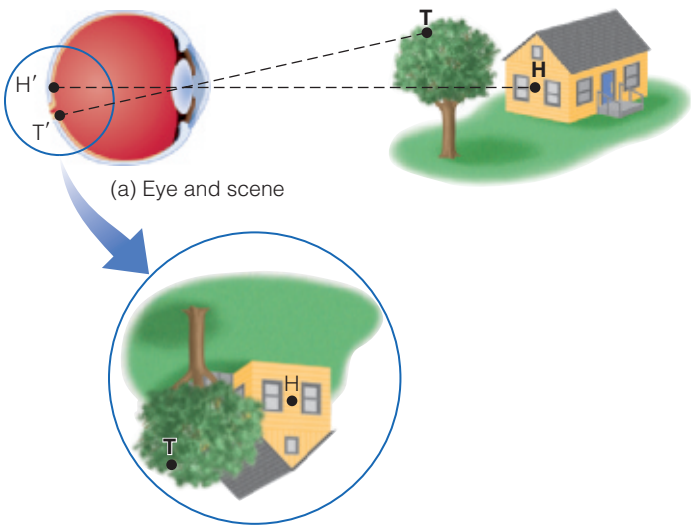

Figure 10.2 (a) In the scene, the house is farther away than the tree, but images of points H on the house and T on the tree fall on points H′ and T′ on the two-dimensional surface of the retina on the back of the eye. (b) These two points on the retinal image, considered by themselves, do not tell us the distances of the house and the tree.

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2. *Monocular.* Cues based on the visual information available within one eye.
3. *Binocular.* Cues that depend on visual information within both eyes.

10.2 Oculomotor Cues

The **oculomotor cues** are created by (1) **convergence**, the inward movement of the eyes that occurs when we look at nearby objects, and (2) **accommodation**, the change in the shape of the lens that occurs when we focus on objects at various distances. The idea behind these cues is that we can *feel* the inward movement of the eyes that occurs when the eyes converge to look at nearby objects, and we feel the tightening of eye muscles that change the shape of the lens to focus on a nearby object. You can experience the feelings in your eyes associated with convergence and accommodation by doing the following demonstration.

DEMONSTRATION | Feelings in Your Eyes

Look at your finger as you hold it at arm's length. Then, as you slowly move your finger toward your nose, notice how you feel your eyes looking inward and become aware of the increasing tension inside your eyes.

The feelings you experience as you move your finger closer are caused by (1) the change in convergence angle as your eye muscles cause your eyes to look inward, as in **Figure 10.3a**, and (2) the change in the shape of the lens as the eye accommodates to focus on a near object (see Figure 3.9, page 44). If you move your finger farther away, the lens flattens, and your eyes move away from the nose until they are both looking straight ahead, as in **Figure 10.3b**. Convergence and accommodation indicate when an object is close; they are useful up to a distance of about arm's length, with convergence being the more effective of the two (Cutting & Vishton, 1995; Mon-Williams & Tresilian, 1999; Tresilian et al., 1999).

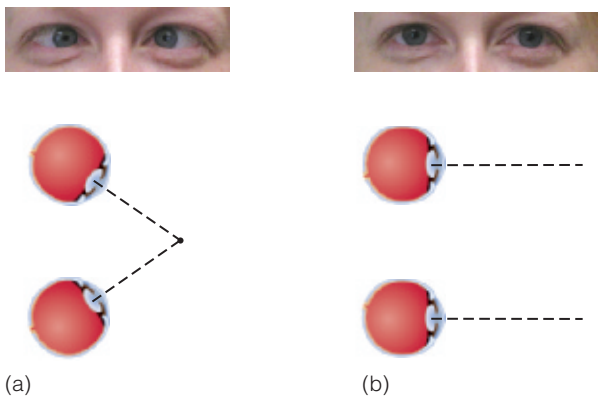

Figure 10.3 (a) Convergence of the eyes occurs when a person looks at something that is very close. (b) The eyes look straight ahead when the person observes something that is far away.

10.3 Monocular Cues

Monocular cues work with only one eye. They include *accommodation*, which we have described under oculomotor cues; *pictorial cues*, which are sources of depth information in a two-dimensional picture; and *movement-based cues*, which are sources of depth information created by movement.

Pictorial Cues

Pictorial cues are sources of depth information that can be depicted in a picture, such as the illustrations in this book or an image on the retina (Goldstein, 2001).

Occlusion We have already described the depth cue of occlusion. Occlusion occurs when one object hides or partially hides another from view. The partially hidden object is seen as being farther away, so the mountains in **Figure 10.4** are perceived as being farther away than the cactus and the hill. Note that occlusion does not provide precise information about an object's distance. It simply indicates that the object that is partially covered is farther away than another object, but from occlusion alone we can't tell how much farther.

Relative Height In the photograph of the scene in **Figure 10.4a**, some objects are near the bottom of the frame and others nearer the top. The height in the frame of the photo corresponds to the height in our field of view, and objects that are higher in the field of view are usually farther away. This is illustrated in **Figure 10.4b**, in which dashed lines 1, 2, and 3 have been added under the front motorcycle, the rear motorcycle, and one of the telephone poles. Notice that dashed lines higher in the picture are under objects that are farther away. You can demonstrate the "higher is farther" principle by looking out at a scene and placing your finger at the places where objects contact the ground. When you do this, you will notice that if all the objects are on a flat surface (no hills!), your finger is higher for farther objects. According to the cue of **relative height**, objects with their bases closer to the horizon are usually seen as being more distant. This means that being *higher* in the field of view causes objects on the *ground* to appear farther away (see lines 1, 2, and 3 in Figure 10.4b), whereas being *lower* in the field of view causes objects in the *sky* to appear farther away (see lines 4 and 5).

Familiar and Relative Size We use the cue of **familiar size** when we judge distance based on our prior knowledge of the sizes of objects. We can apply this idea to the coins in **Figure 10.5a**. If you are influenced by your knowledge of the actual size of dimes, quarters, and half-dollars (**Figure 10.5b**), you might say that the dime is closer than the quarter. An experiment by William Epstein (1965) shows that under certain conditions, our knowledge of an object's size influences our perception of that object's distance (see also McIntosh & Lashley, 2008). The stimuli in Epstein's experiment were equal-sized photographs of a dime, a quarter, and a half-dollar (Figure 10.5a), which were positioned the same distance from an observer. By placing

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(a)

(b)

Figure 10.4 (a) A scene in Tucson, Arizona, containing a number of depth cues: occlusion (the cactus on the right occludes the hill, which occludes the mountain); relative height (the far motorcycle is higher in the field of view than the closer one); relative size (the far motorcycle and telephone pole are smaller than the near ones); and perspective convergence (the sides of the road converge in the distance). (b) 1, 2, and 3 indicate the increasing height in the field of view of the bases of the motorcycles and the far telephone pole, which reveals that being higher in the field of view causes objects on the ground to appear farther away; 4 and 5 reveal that being *lower* in the field of view causes objects in the *sky* to appear farther away, so cloud 5 appears farther from the viewer than cloud 4.

these photographs in a darkened room, illuminating them with a spot of light, and having subjects view them with one eye, Epstein created the illusion that these pictures were real coins.

When the observers judged the distance of each of the coin photographs, they estimated that the dime was closest, the quarter was farther than the dime, and the half-dollar was the farthest of all. Thus, the observers' judgments were influenced by their knowledge of the sizes of these coins. This result does not occur, however, when observers view the scene with both eyes, because, as we will see when we discuss binocular (two-eyed) vision, the use of two eyes provides information indicating the coins are at the same distance. The cue of familiar size is therefore most effective when other information about depth is minimized (see also Coltheart, 1970; Schiffman, 1967).

A depth cue related to familiar size is **relative size**. According to the cue of relative size, when two objects are known to be of equal physical size, the one that is farther away will take up less of your field of view than the one that is closer. For example, knowing (or assuming) that the two telephone poles, or the two motorcycles, in Figure 10.4 are about the same size, we can determine which pole, or motorcycle, is closer than the other.

Perspective Convergence When you look down parallel railroad tracks that appear to converge in the distance, you are experiencing **perspective convergence**. This cue was often used by Renaissance artists to add to the impression of depth in their paintings, as in Pietro Perugino's painting in **Figure 10.6**. Notice that in addition to the perspective

(a)

(b)

Figure 10.5 (a) Photographs similar to those used in Epstein's (1965) familiar-size experiment. Each coin was photographed to be the same size as a real quarter. (b) The actual size of a dime, quarter, and half-dollar.

PRISMA ARCHIVO / Alamy Stock Photo

Figure 10.6 Pietro Perugino, *Christ Handing the Keys to St. Peter* (Sistine Chapel). The convergence of lines on the plaza illustrates perspective convergence. The sizes of the people in the foreground and middle ground illustrate relative size.

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convergence provided by the lines on the plaza, Perugino has included people in the middle ground, further enhancing the perception of depth through the cue of relative size. Figure 10.4 illustrates both perspective convergence (the road) and relative size (the motorcycles) in our Tucson mountain scene.

Perspective Atmospheric perspective occurs because the farther away an object is, the more air and particles (dust, water droplets, airborne pollution) we have to look through, so that distant objects appear less sharp than nearer objects and sometimes have a slight blue tint. **Figure 10.7** illustrates atmospheric perspective. The details in the foreground are sharp and well defined, but details become less and less visible as we look farther into the distance.

The reason that farther objects look bluer is related to the reason the sky appears blue. Sunlight contains a distribution of all of the wavelengths in the spectrum, but the atmosphere preferentially scatters short-wavelength light, which appears blue. This scattered light gives the sky its blue tint and also creates a veil of scattered light between us and objects we are looking at. The blueness becomes obvious, however, only when we are looking through a large distance or when there are many particles in the atmosphere to scatter the light.

If, instead of viewing this cliff along the coast of Maine, you were standing on the moon, where there is no atmosphere and hence no atmospheric perspective, far craters would not look blue and would look just as clear as near ones. But on Earth, there is atmospheric perspective, with the exact amount depending on the nature of the atmosphere.

Texture Gradient When a number of similar objects are equally spaced throughout a scene, as in **Figure 10.8**, they create a texture gradient, which results in a perception of depth, with elements seen as being spaced more closely being perceived as farther.

Bruce Goldstein

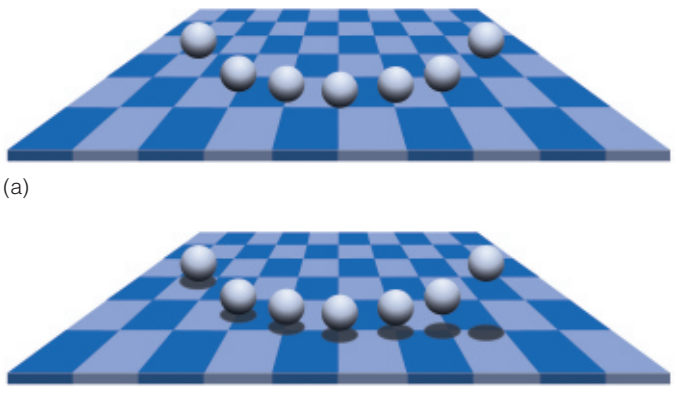
Figure 10.7 A scene on the coast of Maine showing the effect of atmospheric perspective.

Bruce Goldstein

Figure 10.8 A photograph taken in Death Valley, in which the decrease in spacing of the elements with increasing distance illustrates a texture gradient.

Shadows Shadows—decreases in light intensity caused by the blockage of light—can provide information regarding the locations of these objects. Consider, for example, **Figure 10.9a**, which shows seven spheres and a checkerboard. In this picture, the location of the spheres relative to the checkerboard is unclear. They could be resting on the surface of the checkerboard or floating above it. But adding shadows, as shown in **Figure 10.9b**, makes the spheres' locations clearer—the ones on the left are resting on the checkerboard, and the ones on the right are floating above it. This illustrates how shadows can help determine the location of objects (Mamassian, 2004; Mamassian et al., 1998).

Shadows also enhance the three-dimensionality of objects. For example, shadows make the circles in Figure 10.9 appear spherical and help define some of the contours in the mountains in **Figure 10.10**, which appear three-dimensional in the early morning when there are shadows (**Figure 10.10a**), but



(a)

(b)

Figure 10.9 (a) Where are the spheres located in relation to the checkerboard? (b) Adding shadows makes their location clearer. (Courtesy of Pascal Mamassian)

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(a) (b)

Bruce Goldstein

Figure 10.10 (a) Early morning shadows emphasize the mountain's contours. (b) When the sun is overhead, the shadows vanish and it becomes more difficult to see the mountain's contours.

flat in the middle of the day when the sun is directly overhead and there are no shadows (**Figure 10.10b**).

Motion-Produced Cues

All of the cues we have described so far work if the observer is stationary. But once we start moving, new cues emerge that further enhance our perception of depth. We will describe two motion-produced cues: (1) motion parallax and (2) deletion and accretion.

Motion Parallax Motion parallax occurs when, as we move, nearby objects appear to glide rapidly past us, but more distant objects appear to move more slowly. Thus, when you look out the side window of a moving car or train, nearby objects appear to speed by in a blur, whereas objects that are farther away may appear to be moving only slightly. Also, if, when looking out the window, you keep your eyes fixed on one object, objects farther and closer than the object you are looking at appear to move in opposite directions.

We can understand why motion parallax occurs by noting how the image of a near object (the tree in **Figure 10.11a**) and a far object (the house in **Figure 10.11b**) move across the retina as an eye moves from position 1 to position 2 without rotating. First let's consider the tree: Figure 10.11a shows one eye that moves from 1 to 2, so the tree's image moves all the way across the retina from T_1 to T_2, as indicated by the dashed arrow. Figure 10.11b shows that the house's image moves a shorter distance, from H_1 to H_2. Because the image of the tree travels a larger distance across the retina than the house, in the same amount of time, it appears to move more rapidly.

Motion parallax is one of the most important sources of depth information for many animals. For example, before jumping out toward an object such as prey, locusts move their body from side to side to create movement of its head to generate motion parallax signals that indicate the distance of their target (Wallace, 1959). By artificially manipulating environmental information in a way that alters the motion parallax signals obtained by a locust, researchers can "trick" the animal into either jumping short of, or beyond, their intended target (Sobel, 1990). The information provided by motion parallax has been used to enable human-designed mechanical robots to determine how far they are from obstacles as they navigate through the environment (Srinivasan & Venkatesh, 1997). Motion parallax is also widely used to create an impression of depth in cartoons and video games.

Deletion and Accretion As an observer moves sideways, some things become covered, and others become uncovered. Try the following demonstration.

DEMONSTRATION | Deletion and Accretion

Close one eye. Position your hands as shown in **Figure 10.12**, so your right hand is at arm's length and your left hand at about half that distance, just to the left of the right hand. Then as you look at your right hand, move your head sideways to the left, being sure to keep your hands still. As you move your head, your left hand appears to cover your right hand. This covering of the farther right hand is deletion. If you then move your head back to the right, the nearer hand moves back and uncovers the right hand. This uncovering of the far hand is accretion. Deletion and accretion occur all the time as we move through the environment and create information that the object or surface being covered and uncovered is farther away (Kaplan, 1969).

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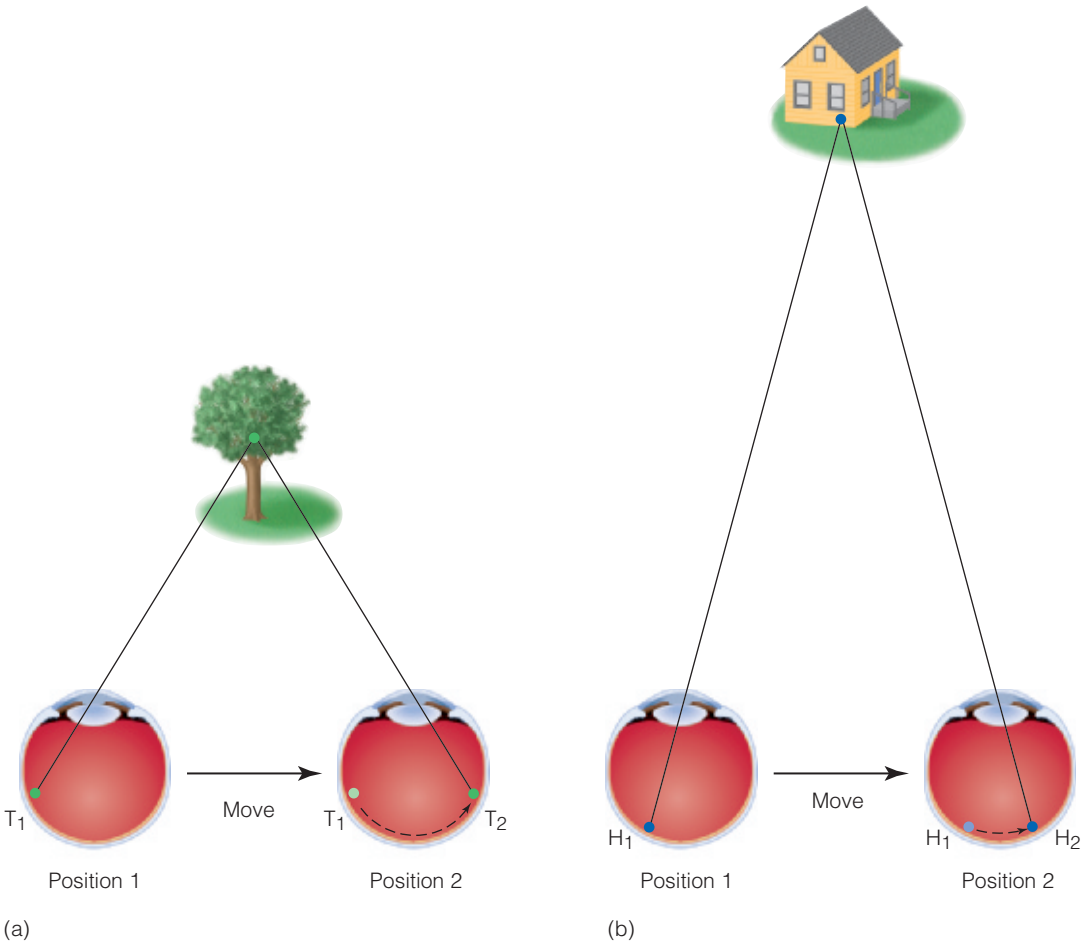

Figure 10.11 One eye moving past (a) a nearby tree; (b) a faraway house. Because the tree is closer, its image moves farther across the retina than the image of the house.

Figure 10.12 Position of the hands for the "Deletion and Accretion" demonstration. See text for explanation.

Integrating Monocular Depth Cues Our discussion so far has described a number of the monocular cues that contribute to our perception of depth. But it is important to understand that each of these cues gives us "best guess" information regarding object depth and that each cue can, by itself, be uninformative in certain situations. For example, relative height is most useful when objects are on a flat plane and we can see where they touch the ground, shadow is most useful if the scene is illuminated at an angle, familiar size is most useful if we have prior knowledge of the objects' sizes, and so forth. Furthermore, as shown in **Table 10.1**, monocular depth cues work over different distances: some only at close range (accommodation, convergence); some at close and medium ranges (motion parallax, deletion and accretion); some at long range (atmospheric perspective, relative height, texture gradients); and some at the whole range of depth perception (occlusion, relative size; Cutting & Vishton, 1995). Thus, for a nearby object, we don't look for atmospheric perspective but instead rely more on convergence, occlusion, or relative size information. Additionally, some depth cues only provide information on relative depth (**Table 10.1a**) while others can contribute to a more precise determination of actual depth (**Table 10.1b**). No depth cue is perfect. No depth cue is applicable to every

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Table 10.1a Cues That Indicate Relative Depth

DEPTH CUE	0–2 METERS	2–20 METERS	ABOVE 20 METERS
Occlusion	√	√	√
Deletion & accretion		√	√
Relative height		√	√
Atmospheric perspective			√

Table 10.1b Cues That Contribute to Determination of Actual Depth

DEPTH CUE	0–2 METERS	2–20 METERS	ABOVE 20 METERS
Relative size	√	√	√
Texture gradients		√	√
Motion parallax	√	√	
Accommodation	√		
Convergence	√		

situation. But by combining different depth cues when they are available, we can achieve a reasonable interpretation of depth.

10.4 Binocular Depth Information

The power of monocular cues to signal depth is plain to see when you close one eye. When you do so, you can still tell what is near and what is far away. However, closing one eye removes some of the information that your brain uses to compute the depth of objects. Two-eyed depth perception involves mechanisms that take into account differences in the images formed on the left and right eyes. The following demonstration illustrates these differences.

DEMONSTRATION | Two Eyes: Two Viewpoints

Close your right eye. Hold a finger on your left hand at arm's length. Position a right-hand finger about a foot away, so it covers the other finger. Then open the right eye and close the left. When you switch eyes, how does the position of your front finger change relative to the rear finger?

When you switched from looking with your left eye to your right, you probably noticed that the front finger appeared to move to the left relative to the far finger. **Figure 10.13** diagrams what happened on your retinas. The solid line in **Figure 10.13a** shows that when the left eye was open, the images of the near and far fingers were lined up with the same place on the retina. This occurred because you were looking directly at both objects, so both images would fall on the foveas of the left eye. The solid lines in **Figure 10.13b** show that when the right eye was open, the image of the far finger still fell on the fovea because you were looking at it, but the image of the near finger was now off to the side.

Whereas the fingers were lined up relative to the left eye, the right eye "looks around" the near finger, so the far finger becomes visible. These different viewpoints for the two eyes are the basis of **stereoscopic vision**, which creates **stereoscopic depth perception**—depth perception created by input from both eyes. Before describing these mechanisms, we will consider what it means to say that stereoscopic depth perception is qualitatively different from monocular depth perception.

Seeing Depth With Two Eyes

One way to appreciate the qualitative difference between monocular depth perception and stereoscopic depth perception is to consider the story of Susan Barry, a neuroscientist at Mt. Holyoke College. Her story—first described by neurologist Oliver Sacks, who dubbed her "Stereo Sue" (Sacks, 2006, 2010), and then in her own book, *Fixing My Gaze* (Barry, 2011)—begins with Susan's childhood eye problems. She was cross-eyed, so when she looked at something with one eye, the other eye would be looking somewhere else. For most people, both eyes aim at the same place and work in coordination with each other, but in Susan's case, the input was uncoordinated. Situations such as this, along with a condition called "walleye" in which the eyes look outward, are forms of **strabismus**, or misalignment of the eyes. When this occurs, the visual system suppresses vision in one of the eyes to avoid double vision, so the person sees the world with only one eye at a time.

Susan had a number of operations as a child that made her strabismus less noticeable to others, but her vision was still dominated by one eye. Although her perception of depth was only achieved through monocular cues, she was able to get along quite well. She could drive, play softball, and do most of the things people with stereoscopic vision can do. For example, she describes her vision in a college classroom as follows:

> I looked around. The classroom didn't seem entirely flat to me. I knew that the student sitting in front of me was located between me and the blackboard because the student blocked my view of the blackboard. When I looked outside the classroom window, I knew which trees were located further away because they looked smaller than the closer ones. (Barry, 2011, Chapter 1)

Although Susan could use these monocular cues to perceive depth, her knowledge of the neuroscience literature and various other experiences she describes in her book led her to realize that she was still seeing with one eye despite her childhood operations. She therefore consulted an optometrist, who confirmed her one-eyed vision and assigned eye exercises designed to improve the coordination between her two eyes. These exercises enabled Susan to coordinate her eyes, and one day after leaving the optometrist's office, she had her first experience with stereoscopic depth perception, which she describes as follows:

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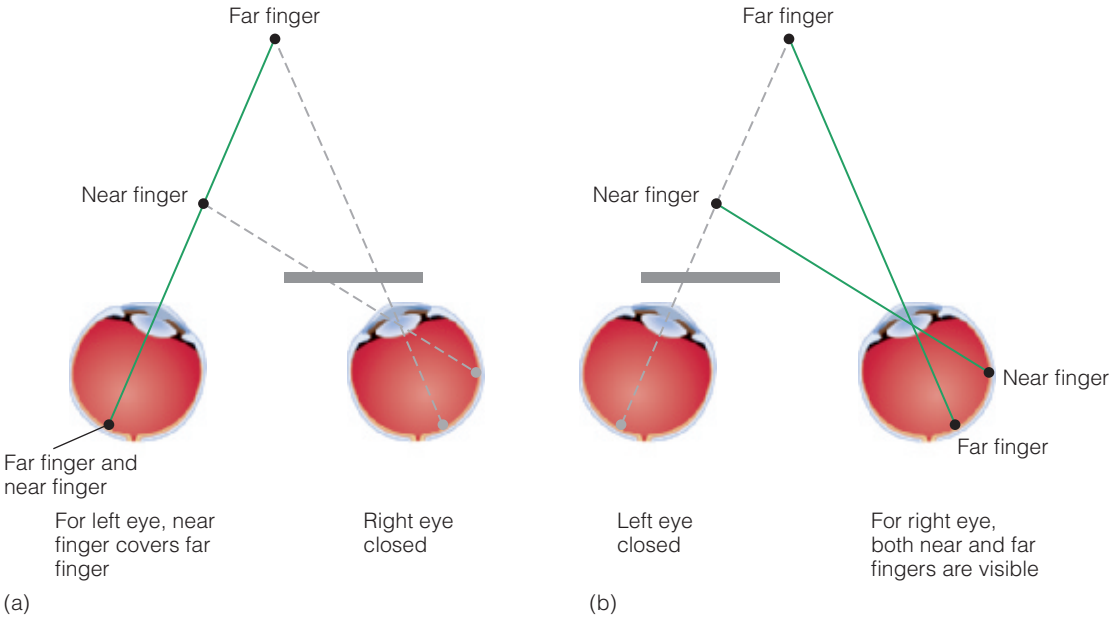

Figure 10.13 Location of images on the retina for the "Two Eyes: Two Viewpoints" demonstration. See text for explanation.

> I got into my car, sat down in the driver's seat, placed the key in the ignition, and glanced at the steering wheel. It was an ordinary steering wheel against an ordinary dashboard, but it took on a whole new dimension that day. The steering wheel was floating in its own space, with a palpable volume of empty space between the wheel and the dashboard. I closed one eye and the steering wheel looked "normal" again; that is, it lay flat just in front of the dashboard. I reopened the closed eye, and the steering wheel floated before me. (Barry, 2011, Chapter 6)

From that point on, Susan had many more experiences that astounded her, but it is important to note that Susan didn't suddenly gain stereovision equivalent to that experienced by a person with stereoscopic vision from birth. Her stereovision occurred first for nearby objects and then, as her training progressed, was extended to farther distances. But what she did experience dramatically illustrates the richness that stereoscopic vision adds to the experience of depth perception.

The added experience of depth created by stereoscopic depth perception is also illustrated by the difference between standard movies and 3-D movies. Standard movies, which project images on a flat screen, create a perception of depth based on monocular depth cues like occlusion, relative height, shadows, and motion parallax. Three-dimensional movies add stereoscopic depth perception. This is achieved by using two cameras placed side by side. Like each of your eyes, each camera receives a slightly different view of the scene (**Figures 10.14a** and **10.14b**). These two images are then overlaid on the movie screen (**Figure 10.14c**).

(a) Left camera (b) Right camera (c) Overlay of camera images

Figure 10.14 (a) and (b) 3-D movies are filmed using two side-by-side cameras so that each camera records a slightly different view of the scene. (c) The images are then projected onto the same 2-D surface. Without 3-D glasses, both images are visible to both eyes. 3-D glasses separate the images so that one is only seen by the left eye and the other is only seen by the right eye. When the left and right eyes receive these different images, stereoscopic depth perception occurs.

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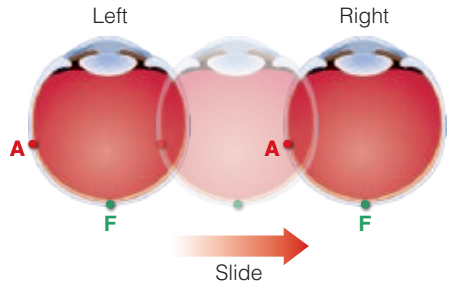

Figure 10.15 Corresponding points on the two retinas. To determine corresponding points, imagine that the left eye is slid on top of the right eye. F indicates the fovea, where the image of an object occurs when an observer looks directly at the object, and A is a point in the peripheral retina. Images on the fovea always fall on corresponding points. Notice that the As, which also fall on corresponding points, are the same distance from the fovea in the left and right eyes.

When wearing 3-D glasses, the lenses separate the two overlapping images so that each eye only receives one of the images. This image separation can be achieved in several ways, but the most common method used in 3-D movies uses polarized light—light waves that vibrate in only one orientation. One image is polarized so its vibration is vertical and the other is polarized so its vibration is horizontal. The glasses you wear have polarized lenses that let only vertically polarized light into one eye and horizontally polarized light into the other eye. Thus, sending these two different views to two different eyes duplicates what happens in the real 3-D world, and suddenly some objects can appear to be recessed behind the screen while others appear to jut far out in front of it.

Binocular Disparity

Binocular disparity, the difference in the images on the left and right retinas, is the basis of stereoscopic vision. We now look more closely at the information on the left and right retinas that the brain uses to create an impression of depth.

Corresponding Retinal Points We begin by introducing corresponding retinal points—points on the retina that would overlap if the eyes were superimposed on each other (**Figure 10.15**). We can illustrate corresponding points by considering what Owen sees in **Figure 10.16a**, when he is looking directly at Julie. **Figure 10.16b** shows where Julie's images are located on Owen's retinas. Because Owen is looking directly at Julie, her images fall on Owen's foveas in both eyes, indicated by the red dots. The two foveas are corresponding points, so Julie's images fall on corresponding points.

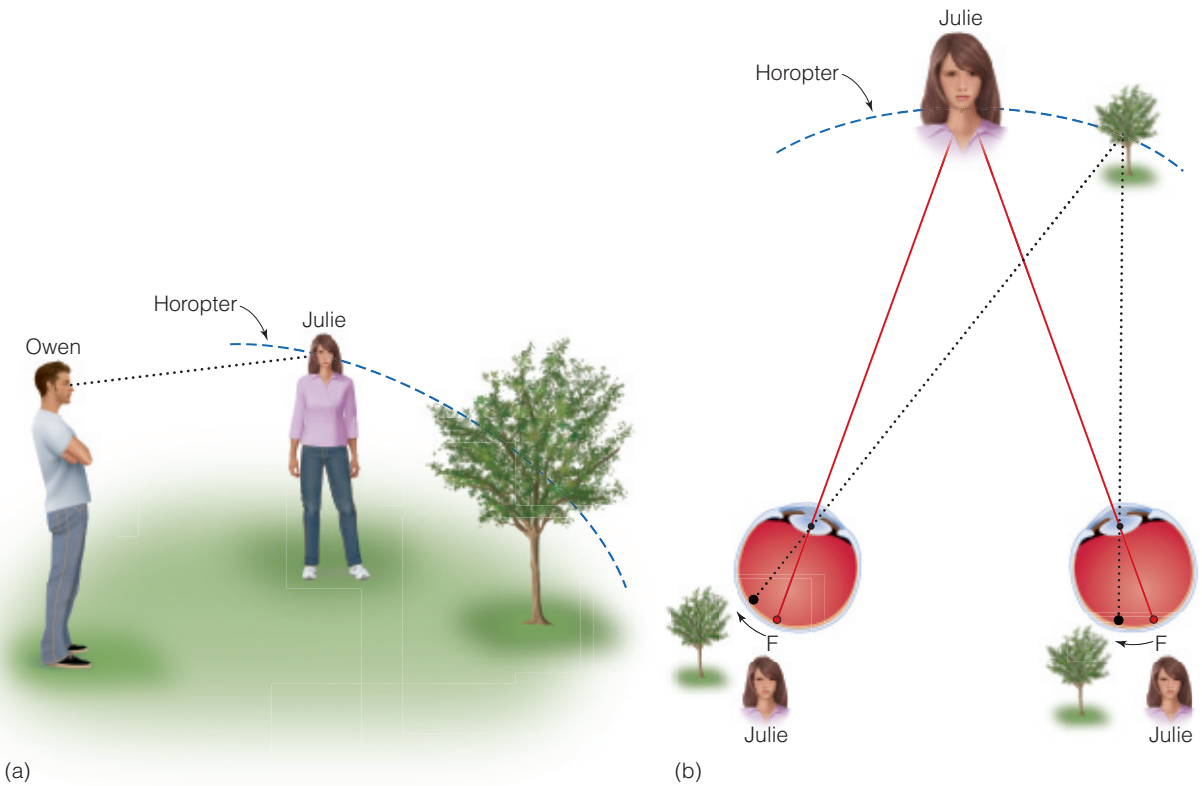

Figure 10.16 (a) Owen is looking at Julie's face, with a tree off to the side. (b) Owen's eyes, showing where the images of Julie and the tree fall on each eye. Julie's images fall on the fovea, so they are on corresponding points. The arrows indicate that the tree's images are located the same distances from the fovea in the two eyes, so they are also on corresponding points. The dashed line in (a) and (b) is the horopter. The images of objects that are on the horopter fall on corresponding points.

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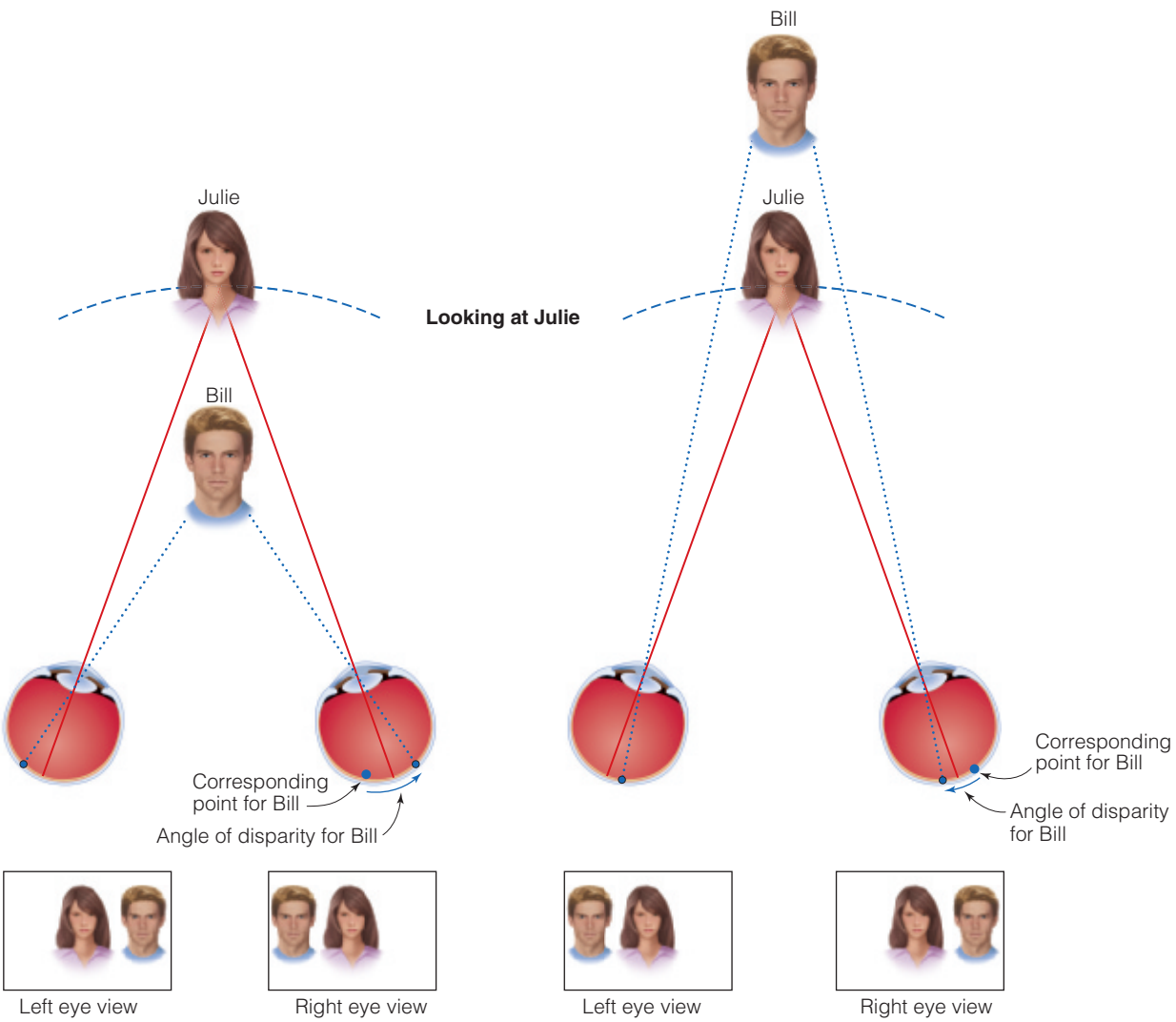
In addition, the images of other objects also fall on corresponding points. Consider, for example, the tree in Figure 10.16b. The tree's images are on the same place relative to the foveas—to the left and at the same distance (indicated by the arrows). This means that the tree's images are on corresponding points. (If you were to slide the eyes on top of each other, Julie's images would overlap, and the tree's images would overlap.) Thus, whatever a person is looking at directly (like Julie) falls on corresponding points, and some other objects (like the tree) fall on corresponding points as well. Julie, the tree, and any other objects that fall on corresponding points are located on a surface called the **horopter**. The blue dashed lines in Figures 10.16a and 10.16b show part of the horopter.

Noncorresponding Points and Absolute Disparity

The images of objects that are *not* on the horopter fall on **noncorresponding points**. This is illustrated in **Figure 10.17a**, which shows Julie again, with her images on corresponding points, and a new character, Bill, who is located in front of the horopter. Because Bill is not on the horopter, his image falls on noncorresponding points in each retina. The degree to which Bill's image *deviates* from falling on corresponding points is called **absolute disparity**. The amount of absolute disparity, called the **angle of disparity**, is indicated by the blue arrow in Figure 10.17a; it is the angle between the corresponding point on the right eye for the left-eye image of Bill (blue dot) and the actual location of the image on the right eye (red dot). **Figure 10.17b** shows that binocular disparity also occurs



(a) Bill is in front of the horopter (b) Bill is behind the horopter

Figure 10.17 (a) When an observer looks at Julie, Julie's images fall on corresponding points. Because Bill is in front of the horopter, his images fall on noncorresponding points. The angle of disparity, indicated by the blue arrow, is determined by measuring the angle between where the corresponding point for Bill's image would be located and where Bill's image is actually located. (b) Disparity is also created when Bill is behind the horopter. The pictures at the bottom of the figure illustrate how the positions of Julie and Bill are seen by each eye.

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when objects are behind the horopter (farther away than a fixated object).

Although objects appearing in front of the horopter (Figure 10.17a) and behind the horopter (Figure 10.17b) both result in retinal disparity, the disparity is somewhat different in the two situations. To understand this difference, let's think about what each eye sees individually in Figures 10.17a and 10.17b.

The pictures at the bottom of Figure 10.17a show what the left and right eyes see when Bill is in front of Julie. In this situation, the left eye sees Bill to Julie's right, while the right eye sees Bill to Julie's left. This pattern of disparity where the left eye sees an object (e.g., Bill) to the right of the observer's fixation point (e.g., Julie) and the right eyes sees that same object to the left of the fixation point is called **crossed disparity** (you can remember this by thinking about the fact that you would need to "cross" your eyes in order to fixate Bill). Crossed disparity occurs whenever an object is closer to the observer than where the observer is looking.

Now let's consider what happens when an object is behind the horopter. The pictures at the bottom of Figure 10.17b show what each eye sees when Bill is behind Julie. This time, the left eye sees Bill to Julie's left and the right eye sees Bill is to Julie's right. This pattern of disparity where the left eye sees an object to the left of the observer's fixation point and the right eyes sees that same object to the right of the fixation point is called **uncrossed disparity** (in order to fixate on Bill you would need to "uncross" your eyes). Uncrossed disparity occurs whenever an object is behind the horopter. Thus, by determining whether an object produces crossed or uncrossed disparity, the visual system can determine whether that object is in front of or behind a person's point of fixation.

Absolute Disparity Indicates Distance From the Horopter Determining whether absolute disparity is crossed or uncrossed indicates whether an object is in front of or behind the horopter. This is of course important information to have, but it provides only part of the story. To perceive depth accurately, we also need to know the distance between an object and the horopter. This information is provided by the amount of disparity associated with an object.

Figure 10.18 shows that the angle of disparity is greater for objects at greater distances from the horopter. The observer is still looking at Julie, and Bill is in front of the horopter where he was in Figure 10.17a, but now we have added Dave, who is located even farther from the horopter than Bill. When we compare Dave's angle of disparity in this figure (large green arrow) to Bill's (small purple arrow), we see that Dave's disparity is greater. The same thing happens for objects farther away than the horopter, with greater distance also associated with greater absolute disparity. The angle of disparity therefore provides information about an object's distance from the horopter, with greater angles of disparity indicating greater distances from the horopter. There is also another type of disparity, called **relative disparity**, which is related to how we judge the distance between two objects. In our discussion, we will continue to focus on absolute disparity.

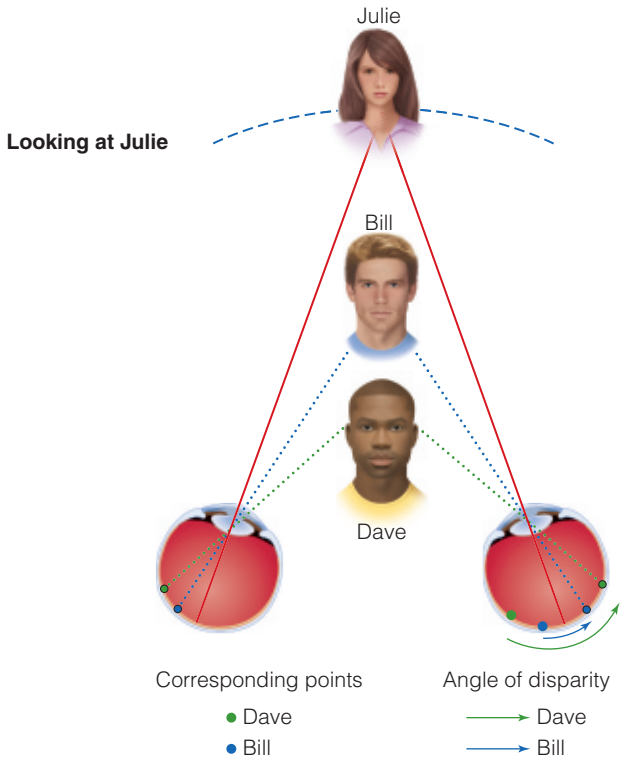

Figure 10.18 Objects that are farther away from the horopter are associated with greater angles of disparity. In this case, both Dave and Bill are in front of the horopter, but Dave is farther from the horopter than Bill, as indicated by comparing the large green arrow (Dave's disparity) to the small purple arrow (Bill's disparity).

Disparity (Geometrical) Creates Stereopsis (Perceptual)

We have seen that disparity information contained in the images on the retinas provides information indicating an object's relative distance from where the observer is looking. Notice, however, that our description of disparity has focused on *geometry*—looking at where objects' images fall on the retina—but has not mentioned *perception*, the observer's experience of an object's depth or its relation to other objects in the environment (**Figure 10.19**). We consider the relationship between disparity and what observers perceive by introducing **stereopsis**—the impression of depth that results from information provided by binocular disparity.

In order to demonstrate that disparity creates stereopsis, we need to isolate disparity information from other depth cues, such as occlusion and relative height, because these other cues can also contribute to our perception of depth. In order to show that disparity alone can result in depth perception, Bela Julesz (1971) created a stimulus called the *random-dot stereogram*, which contains no pictorial cues. By creating stereoscopic images of random-dot patterns, Julesz showed that observers can perceive depth in displays that contain no depth information other than disparity. Two such random-dot patterns, which together constitute a **random-dot stereogram**, are shown in **Figure 10.20**. These patterns were constructed by

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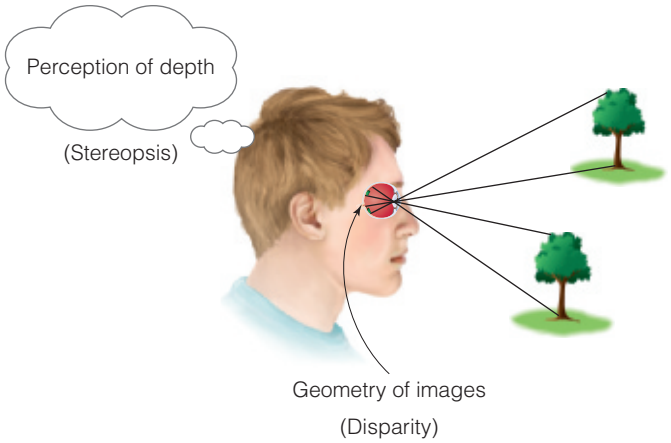


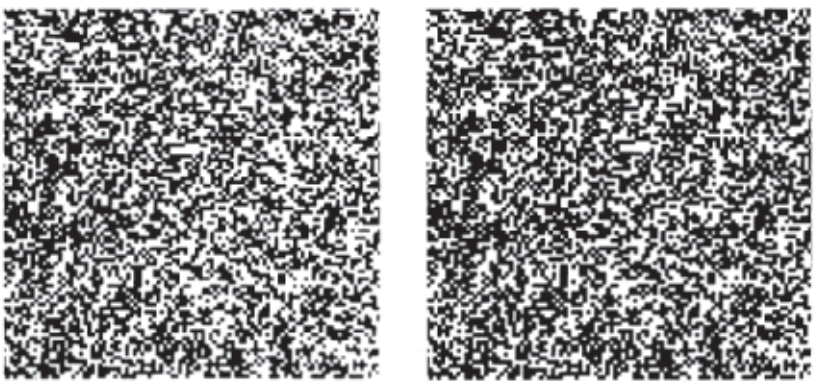
Figure 10.19 Disparity is related to geometry—the locations of images on the retina. Stereopsis is related to perception—the experience of depth created by disparity.

first generating two identical random-dot patterns on a computer and then shifting a square-shaped section of the dots one or more units to the side.

In the stereogram in **Figure 10.20a**, a section of dots from the pattern on the left has been shifted one unit to the right to form the pattern on the right. This shift is too subtle to be seen in the dot patterns, but we can understand how it is accomplished by looking at the diagrams below the dot patterns (**Figure 10.20b**). In these diagrams, the black dots are indicated by 0s, As, and Xs and the white dots by 1s, Bs, and Ys. The As and Bs indicate the square-shaped section where the shift is made in the pattern. Notice that the As and Bs are shifted one unit to the right in the right-hand pattern. The Xs and Ys indicate areas uncovered by the shift that must be filled in with new black dots and white dots to complete the pattern.

As you look at Figure 10.20a on the page, information from both the left and right images travel to both your left and right eyes and it is difficult, if not impossible, to tell that the dots have been shifted. The visual system can, however, detect a difference between these images if we separate the visual information on the page so that the left image is only seen by the left eye and the right image is only seen by the right eye. With two side-by-side images (rather than slightly overlapping as in Figure 10.14c) this separation is accomplished by using a device called a **stereoscope** (**Figure 10.21**) that uses two lenses to focus the left image on the left eye and the right image on the right eye. When viewed in this way, the disparity created by the shifted section results in perception of a small square floating above the background. Because binocular disparity is the only depth information present in these stereograms, disparity alone must be causing the perception of depth.

Psychophysical experiments, particularly those using Julesz's random-dot stereograms, show that retinal disparity



(a)

1	0	1	0	1	0	0	1	0	1
1	0	0	1	0	1	0	1	0	0
0	0	1	1	0	1	1	0	1	0
0	1	0	A	A	B	B	1	0	1
1	1	1	B	A	B	A	0	0	1
0	0	1	A	A	B	A	0	1	0
1	1	1	B	B	A	B	1	0	1
1	0	0	1	1	0	1	1	0	1
1	1	0	0	1	1	0	1	1	1
0	1	0	0	0	1	1	1	1	0

1	0	1	0	1	0	0	1	0	1
1	0	0	1	0	1	0	1	0	0
0	0	1	1	0	1	1	0	1	0
0	1	0	Y	A	A	B	B	0	1
1	1	1	X	B	A	B	A	0	1
0	0	1	X	A	A	B	A	1	0
1	1	1	Y	B	B	A	B	0	1
1	0	0	1	1	0	1	1	0	1
1	1	0	0	1	1	0	1	1	1
0	1	0	0	0	1	1	1	1	0

(b)

Figure 10.20 (a) A random-dot stereogram. (b) The principle for constructing the stereogram. See text for explanation.

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(a) (b)

Figure 10.21 Examples of (a) antique and (b) modern stereoscopes.

creates a perception of depth. But before we can fully understand the mechanisms responsible for depth perception, we must answer one more question: How does the visual system match the parts of the images in the left and right eyes that correspond to one another? This is called the **correspondence problem**, and as we will see, it has still not been fully explained.

The Correspondence Problem

Let's return to the stereoscopic images of Figure 10.14c. When we view this image through 3-D glasses (p. 237), we see different parts of the image at different depths because of the disparity between images on the left and right retinas. Thus, the cactus and the window appear to be at different distances when viewed through the glasses because they create different amounts of disparity. But in order for the visual system to calculate this disparity, it must compare the images of the cactus on the left and right retinas and the images of the window on the left and right retinas.

One way the visual system might do this is by matching the images on the left and right retinas on the basis of the specific features of the objects. Explained in this way, the solution seems simple: Most things in the world are quite discriminable from one another, so it is easy to match an image on the left retina with the image of the same thing on the right retina. Returning to Figure 10.14, the upper-left windowpane that falls on the left retina could be matched with the upper-left pane on the right retina, and so on. But determining corresponding points based on object features can't be the whole answer to the correspondence problem, because that strategy won't work for Julesz's random dot stereogram (Figure 10.20).

You can appreciate the problem involved in matching similar parts of a stereogram by trying to match up the points in the left and right images of the stereogram in Figure 10.20a. Most people find this to be an extremely difficult task, involving switching their gaze back and forth between the two pictures and comparing small areas of the pictures one after another. But even though matching similar features on a random-dot stereogram is much more difficult and time-consuming than matching features in the real world, the visual system somehow matches similar parts of the two stereogram images, calculates their disparities, and creates a perception of depth.

From the random-dot stereogram example, it is clear that the visual system accomplishes something rather amazing when it solves the correspondence problem. Researchers in fields as diverse as psychology, neuroscience, mathematics, and engineering have put forth a number of specific proposals, all too complex to discuss here, that seek to explain how the visual system fully solves the correspondence problem (Goncalves & Welchman, 2017; Henricksen et al., 2016; Kaiser et al., 2013; Marr & Poggio, 1979). Despite these efforts, however, a totally satisfactory solution to the correspondence problem has yet to be proposed.

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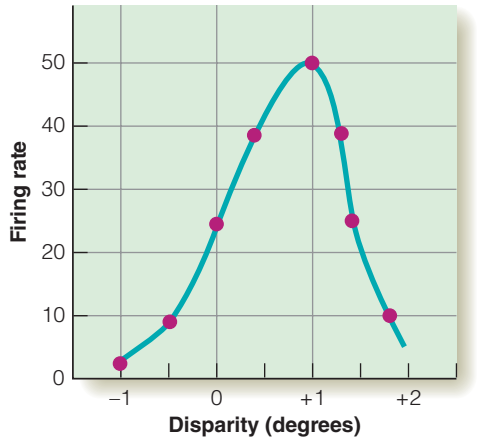

Figure 10.22 Disparity tuning curve for a neuron sensitive to absolute disparity. This curve indicates the neural response that occurs when stimuli presented to the left and right eyes create different amounts of disparity. (From Uka & DeAngelis, 2003)

10.5 The Physiology of Binocular Depth Perception

The idea that binocular disparity provides information about the positions of objects in space implies that there should be neurons that signal different amounts of disparity. These neurons, which are called **binocular depth cells** or **disparity-selective cells,** were discovered when research in the 1960s and 1970s revealed neurons that respond to disparity in the primary visual cortex, area V1 (Barlow et al., 1967; Hubel & Wiesel, 1970). These cells respond best when stimuli presented to the left and right eyes create a specific amount of disparity (Hubel et al., 2015; Uka & DeAngelis, 2003). **Figure 10.22** shows a **disparity tuning curve** for one of these neurons. This particular neuron responds best when the left and right eyes are stimulated to create an absolute disparity of about 1 degree.

The relationship between binocular disparity and the firing of binocular depth cells is an example of the stimulus–physiology relationship in the diagram of the perceptual process in **Figure 10.23** (relationship B). This diagram, which we introduced in Chapter 1 (see Figure 1.13, page 12) and repeated in Chapter 8 (see Figure 8.12, page 184), also depicts two other relationships. The stimulus–perception relationship (A) is the relationship between binocular disparity and the perception of depth. The final relationship, between physiology and perception (C), involves demonstrating a connection between disparity-selective neurons and depth perception. This has been achieved in a number of ways.

An early demonstration of a connection between binocular neurons and perception involved the selective rearing procedure we described in our discussion of the relationship between feature detectors and perception in Chapter 4 (see page 72). Applying this procedure to depth perception, Randolph Blake and Helmut Hirsch (1975) reared cats so that their vision was alternated between the left and right eyes every other day during the first 6 months of their lives. After this 6-month period of presenting stimuli to just one eye at a time, Blake and Hirsch recorded from neurons in the cat's visual cortex and found that (1) these cats had few binocular neurons and (2) they performed poorly on the depth perception task. Thus, eliminating binocular neurons eliminates stereopsis and confirms what everyone suspected all along—that disparity-selective neurons are responsible for stereopsis (also see Olson & Freeman, 1980).

Early research on disparity-selective neurons focused on neurons in the primary visual receiving area, V1. But later research has shown that neurons sensitive to disparity are found in many areas outside V1 (Minini et al., 2010; Parker et al., 2016) (**Figure 10.24**). Gregory DeAngelis and coworkers

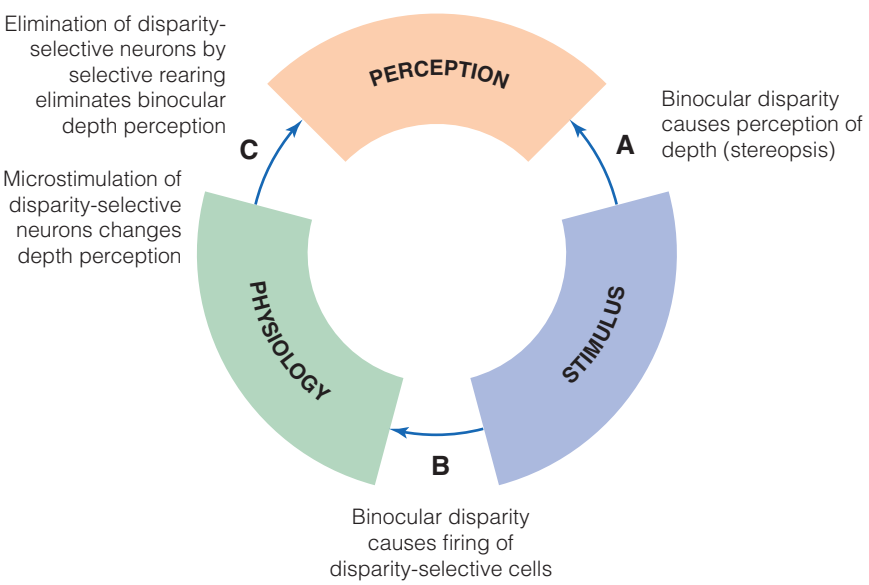

Figure 10.23 The three relationships in the perceptual process, as applied to binocular disparity. We have described experiments relating disparity to perception (A) and relating disparity to physiological responding (B). The final step is to determine the relationship between physiological responses to disparity and perception (C). This has been studied by selective rearing, which eliminates disparity-selective neurons, and by microstimulation, which activates disparity-selective neurons.

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Minini et al., 2010

Figure 10.24 fMRI responding to disparity in random-dot stereograms, as indicated by the colored areas, shows that responses to stereoscopic depth is widespread in the cortex, including much of the visual cortex in the occipital lobe and parts of the parietal cortex.

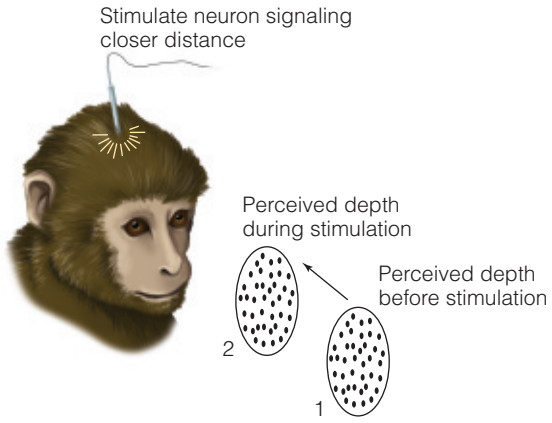

Figure 10.25 While the monkey was observing a random-dot stereogram, DeAngelis and coworkers (1998) stimulated neurons in the monkey's cortex that were sensitive to a particular amount of disparity. This stimulation shifted the monkey's perception of the depth of the field of dots from position 1 to position 2.

(1998) studied disparity-selective neurons in area MT, by using microstimulation (see Method: Microstimulation, Chapter 8, page 185) to pass an electrical charge through neurons in that area. Because neurons that are sensitive to the same disparities tend to be organized in clusters, stimulating one of these clusters activates a group of neurons that respond best to a specific disparity (Hubel et al., 2015).

DeAngelis trained monkeys to indicate the depth created by presenting images with different disparities. Presumably, the monkey perceived depth because the disparate images on the monkey's retinas activated disparity-selective neurons in the cortex. But when DeAngelis stimulated neurons that were tuned to a disparity different from what was indicated by the images on the retina, the monkey shifted its depth judgment toward the disparity signaled by the stimulated neurons (**Figure 10.25**). The results of the selective rearing and the microstimulation experiments indicate that binocular depth cells are a physiological mechanism responsible for depth perception, thus providing the physiology–perception relationship of the perceptual process in Figure 10.23.

10.6 Depth Information Across Species

Humans make use of a number of different sources of depth information in the environment. But what about other species? Many animals have excellent depth perception. Cats leap on their prey; monkeys swing from one branch to the next; and a male housefly maintains a constant distance of about 10 cm as it follows a flying female. There is no doubt that many animals are able to judge distances in their environment, but what depth information do they use? Considering the information used by different animals, we find that animals use the entire range of cues described in this chapter. Some animals use many cues, and others rely on just one or two.

To make use of binocular disparity, an animal must have eyes that have overlapping visual fields. Thus, animals such as cats, monkeys, and humans that have frontal eyes (**Figure 10.26**), which result in overlapping fields of view, can use disparity to perceive depth.

Animals in addition to cats, monkeys, and humans that use disparity to perceive depth include owls (Willigen, 2011), horses (Timney & Keil, 1999), and insects (Rossel, 1983). To

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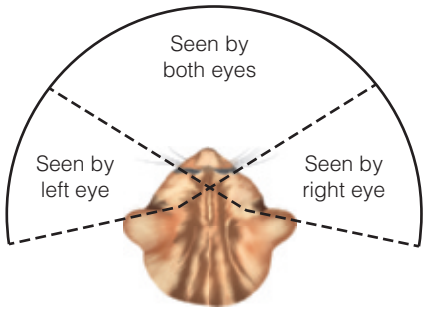

Figure 10.26 Frontal eyes, such as those of the cat, have overlapping fields of view that provide good stereoscopic depth perception.

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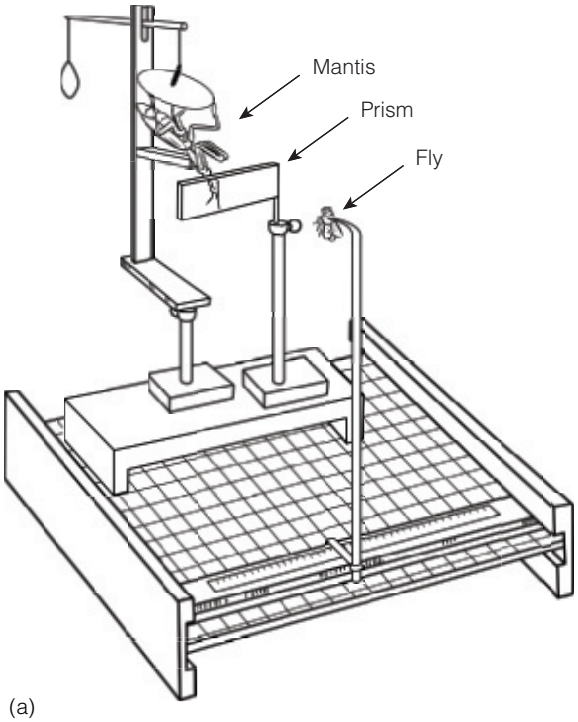

(a)

"Newcastle University, UK"

(b)

Figure 10.27 (a) The apparatus used by Rossel (1983) to determine if the praying mantis is sensitive to binocular disparity. The mantis is upside down, with prisms in front of its eyes. A fly is mounted in front of the mantis. (b) A mantis fitted with red and purple glasses that enable it to perceive stereo projections on a screen in three dimensions.

determine if insects use disparity to perceive depth Samuel Rossel (1983) used the praying mantis, an insect with large overlapping eye fields. He positioned the mantis upside down (something mantises do often) and placed prisms in front of its eyes, as shown in **Figure 10.27a**. When Rossel moved a fly toward the mantis and determined when the mantis reached for the fly with its legs—a response called *striking*—he found that the mantis' striking was determined by the fly's apparent distance as determined by the strength of the prisms. In other words, the degree of disparity was controlling the mantis' perception of the fly's distance.

A more recent mantis experiment created a "mantis cinema" in which the mantis wore red–purple glasses, as in **Figure 10.27b**. This arrangement, which has the advantage of being able to control disparity by varying the separation of the red and purple images on the projection screen, has confirmed and extended Rossel's findings (Nityanada et al., 2016, 2018).

Animals with **lateral eyes**, such as the rabbit (**Figure 10.28**), have much less overlap and therefore can use disparity only in the small area of overlap to perceive depth. Note, however, that in sacrificing binocular disparity, animals with lateral eyes gain a wider field of view—something that is extremely important

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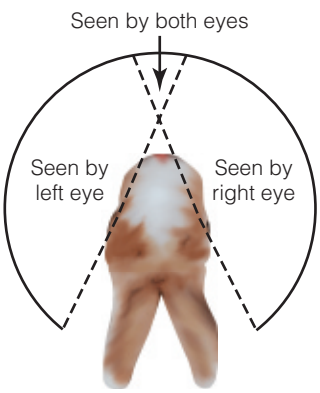

Figure 10.28 Lateral eyes, such as those of the rabbit, provide a panoramic view but stereoscopic depth perception occurs only in the small area of overlap.

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for animals that need to constantly be on the lookout for predators.

The pigeon is an example of an animal with lateral eyes that are placed so that the visual fields of the left and right eyes overlap only in a 35-degree area surrounding the pigeon's beak. This overlapping area, however, happens to be exactly where pieces of grain would be located when the pigeon is pecking at them, and psychophysical experiments have shown that the pigeon does have a small area of binocular depth perception right in front of its beak (McFadden, 1987; McFadden & Wild, 1986).

Motion parallax is probably insects' most important method of judging distance, and they use it in a number of different ways (Collett, 1978; Srinivasan & Venkatesh, 1997). For example, we've mentioned that locusts use motion parallax information generated by moving their heads from side to side, as they observe potential prey (p. 234). T. S. Collett (1978) measured a locust's "peering amplitude"—the distance of this side-to-side sway—as it observed prey at different distances, and found that the locust swayed more when targets were farther away. Since more distant objects move less across the retina than nearer objects for a given amount of observer movement, a larger sway would be needed to cause the image of a far object to move the same distance across the retina as the image of a near object. The locust may therefore be judging distance by noting how much sway is needed to cause the image to move a certain distance across its retina (also see Sobel, 1990).

These examples show how depth can be determined from different sources of information in light. But bats use a form of energy we usually associate with sound to sense depth. Bats sense objects by using a method similar to the sonar system used in World War II to detect underwater objects such as submarines and mines. *Sonar*, which stands for *so*und *na*vigation and *r*anging, works by sending out pulses of sound and using information contained in the echoes of this sound to determine the location of objects. Donald Griffin (1944) coined the term **echolocation** to describe the biological sonar system used by bats to avoid objects in the dark.

Bats emit pulsed sounds that are far above the upper limit of human hearing, and they sense objects' distances by noting the interval between when they send out the pulse and when they receive the echo (**Figure 10.29**). Since they use sound echoes to sense objects, they can avoid obstacles even when it is totally dark (Suga, 1990). Although we don't have any way of knowing what the bat experiences when these echoes return, we do know that the timing of these echoes provides the information the bat needs to locate objects in its environment. (See the discussion of human echolocation in Chapter 12, page 307. Also see von der Emde et al., 1998, for a description of how electric fish sense depth based on "electrolocation.")

From these examples, we can see that animals use a number of different types of information to determine depth and distance, with the type of information used depending on the animal's specific needs and on its anatomy and physiological makeup.

Figure 10.29 When a bat sends out its pulses, it receives echoes from a number of objects in the environment. This figure shows the echoes received by the bat from (a) a nearby moth; (b) a tree located about 2 meters away; and (c) a house, located about 4 meters away. The echoes from more distant objects take longer to return. The bat locates the positions of objects in the environment by sensing how long it takes the echoes to return.

TEST YOURSELF 10.1

1. What is the basic problem of depth perception, and how does the cue approach deal with this problem?
2. What monocular cues provide information about depth in the environment?
3. What do comparing the experience of "Stereo Sue" and the experience of viewing 3-D and 2-D movies tell us about what binocular vision adds to our perception of depth?
4. What is binocular disparity? What is the difference between crossed and uncrossed disparity? What is the difference between absolute disparity and relative disparity? How are absolute and relative disparity related to the depths of objects in a scene?
5. What is stereopsis? What is the evidence that disparity creates stereopsis?
6. What does perception of depth from a random-dot stereogram demonstrate?
7. What is the correspondence problem? Has this problem been solved?
8. Describe each of the relationships in the perceptual process of Figure 10.23, and provide examples for each relationship that has been determined by psychophysical and physiological research on depth perception.

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9. Describe how frontal eyes determine binocular disparity. Describe the praying mantis experiment. What did it demonstrate?
10. Describe how lateral eyes affect depth perception. Also describe how some insects use motion parallax to perceive depth and how bats use echoes to sense objects.

10.7 Perceiving Size

Now that we have described our perception of depth, we will turn our attention to the perception of size. As we noted at the start of this chapter, size perception and depth perception are related. Consider, for example, the following story based on an actual incident at an Antarctic research facility where a helicopter pilot was flying through whiteout weather conditions:

> As Frank pilots his helicopter across the Antarctic wastes, blinding light, reflected down from thick cloud cover above and up from the pure white blanket of snow below, makes it difficult to see the horizon, details on the surface of the snow, or even up from down. He is aware of the danger because he has known pilots dealing with similar conditions who flew at full power directly into the ice. He thinks he can make out a vehicle on the snow far below, and he drops a smoke grenade to check his altitude. To his horror, the grenade falls only three feet before hitting the ground. Realizing that what he thought was a truck was actually a small box, Frank pulls back on the controls and soars up, his face drenched in sweat, as he comprehends how close he just came to becoming another whiteout fatality.

This account illustrates that our ability to perceive an object's size can sometimes be drastically affected by our ability to perceive the object's distance. A small box seen close up can, in the absence of accurate information about its distance, be misperceived as a large truck seen from far away (**Figure 10.30**). The idea that we can misperceive size when accurate depth information is not present was demonstrated in a classic experiment by A. H. Holway and Edwin Boring (1941).

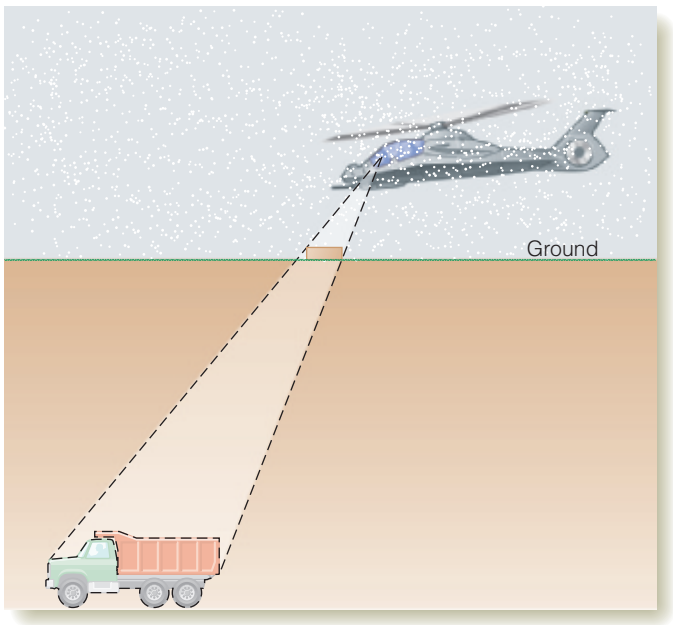

Figure 10.30 When a helicopter pilot loses the ability to perceive distance because of a "whiteout," a small box that is close can be mistaken for a truck that is far away.

The Holway and Boring Experiment

Observers in Holway and Boring's experiment sat at the intersection of two hallways and saw a luminous *test circle* when looking down the right hallway and a luminous *comparison circle* when looking down the left hallway (**Figure 10.31**). The comparison circle was always 10 feet from the observer, but the test circles were presented at distances ranging from 10 feet to 120 feet. An important property of the fixed-in-place comparison circle was that its size could be adjusted. The observer's task on each trial was to adjust the diameter of the comparison circle in the left corridor to match his or her perception of the sizes of the various test circles presented in the right corridor.

An important feature of the test stimuli in the right corridor was that they all cast exactly the same-sized image on the retina. We can understand how this was accomplished by introducing the concept of *visual angle*.

What Is Visual Angle? Visual angle is the angle of an object relative to the observer's eye. **Figure 10.32a** shows how we determine the visual angle of a stimulus (a person, in this example) by extending lines from the person to the lens of the observer's eye. The angle between the lines is the visual angle. Notice that the visual angle depends both on the size of the stimulus and on its distance from the observer; when the person moves closer, as in **Figure 10.32b**, the visual angle becomes larger.

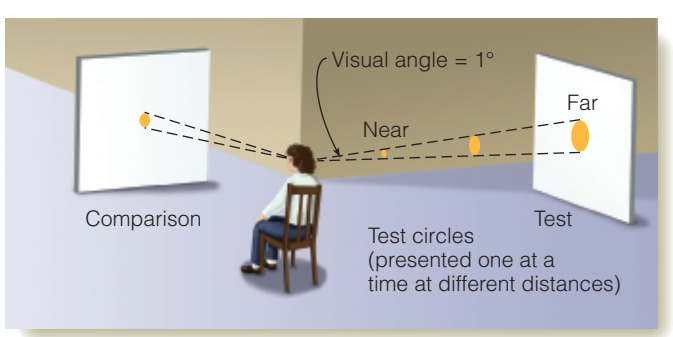

Figure 10.31 Setup of Holway and Boring's (1941) experiment. The observer changes the diameter of the comparison circle in the left corridor to match his or her perception of the size of test circles presented in the right corridor. Each test circle has a visual angle of 1 degree and is presented separately. This diagram is not drawn to scale. The actual distance of the far test circle was 100 feet.

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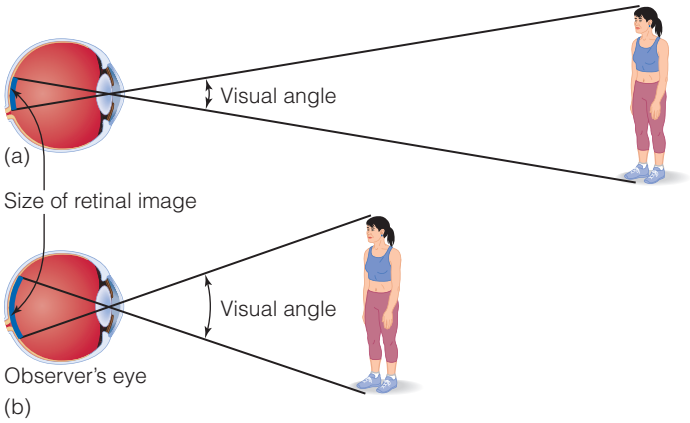
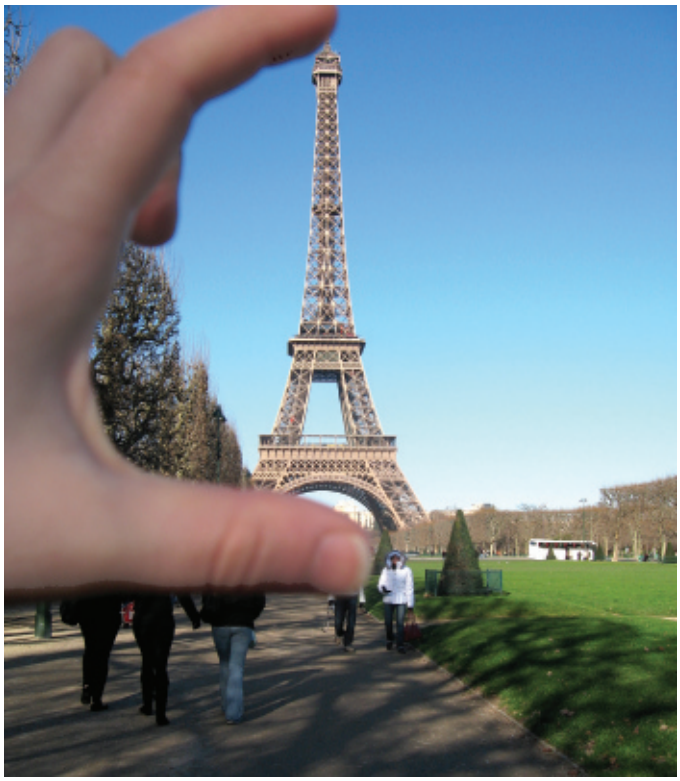


Figure 10.32 (a) The visual angle depends on the size of the stimulus (the woman in this example) and its distance from the observer. (b) When the woman moves closer to the observer, both the visual angle and the size of the image on the retina increase. This example shows that halving the distance between the stimulus and the observer doubles the size of the image on the retina.

The visual angle tells us how large the object will be on the back of the eye. There are 360 degrees around the entire circumference of the eyeball, so an object with a visual angle of 1 degree would take up 1/360 of this circumference—about 0.3 mm in an average-sized adult eye. One way to get a feel for visual angle is to fully extend your arm and look at your thumb, as the woman in **Figure 10.33** is doing. The approximate visual angle of the *width* of the thumb at arm's length is 2 degrees. Thus, an object that is exactly covered by the thumb held at arm's length, such as the phone in Figure 10.33, has a visual angle of approximately 2 degrees.

This "thumb technique" provides a way to determine the approximate visual angle of any object in the environment. It also illustrates an important property of visual angle: A small object that is near (like the thumb) and a larger object that is far (like the phone) can have the same visual angle. A good example of this is illustrated in **Figure 10.34**, which shows a photograph taken by one of my students. To take this picture,



Jennifer Bittel

Figure 10.34 The visual angle between the two fingers is the same as the visual angle of the Eiffel Tower.

the student adjusted the distance between her fingers so that the Eiffel Tower just fit between them. When she did this, the space between her fingers, which were about a foot away, had the same visual angle as the Eiffel Tower, which was hundreds of yards away.

How Holway and Boring Tested Size Perception in a Hallway The idea that objects with different sizes can have the same visual angle was used in the creation of the test circles in Holway and Boring's experiment. As

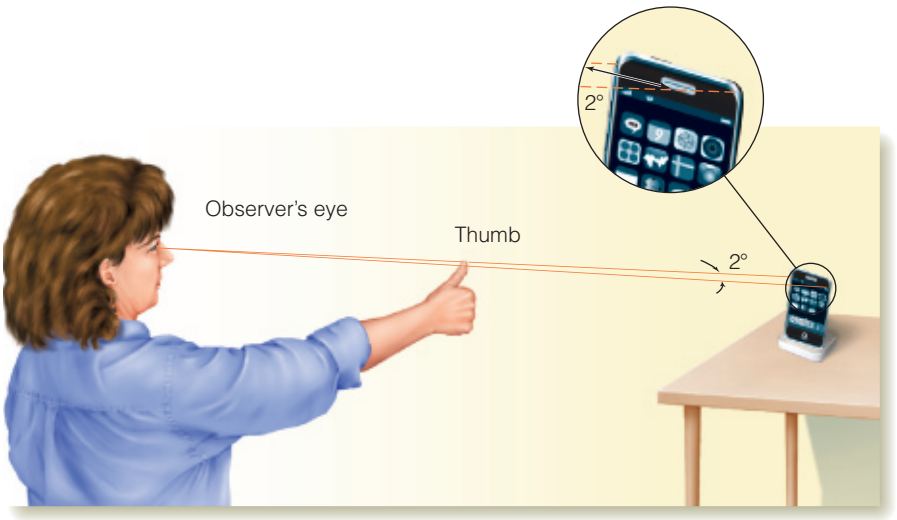


Figure 10.33 The "thumb" method of determining the visual angle of an object. When the thumb is at arm's length, whatever its width covers has a visual angle of about 2 degrees. The woman's thumb covers the width of her iPhone, so the visual angle of the iPhone, from the woman's point of view, is 2 degrees. Note that the visual angle will change if the distance between the woman and the iPhone changes.

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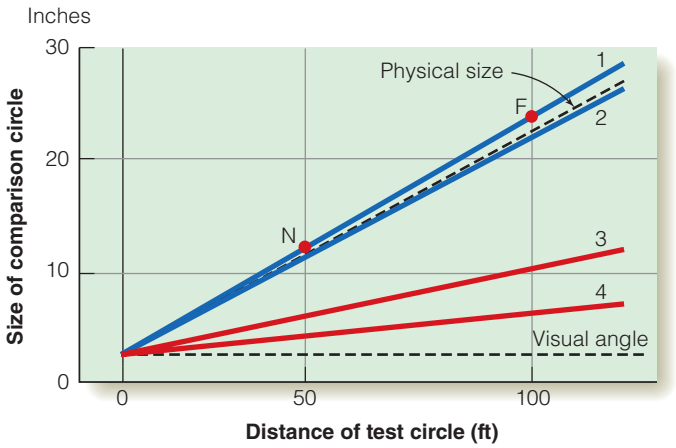

Figure 10.35 Results of Holway and Boring's experiment. The dashed line marked *physical size* is the result that would be expected if the observers adjusted the diameter of the comparison circle to match the actual diameter of each test circle. The line marked *visual angle* is the result that would be expected if the observers adjusted the diameter of the comparison circle to match the visual angle of each test circle.

shown in Figure 10.31, small circles that were positioned close to the observer and larger circles that were positioned farther away all had visual angles of 1 degree. Because objects with the same visual angle create the same-sized image on the retina, all of the test circles had the same-sized image on the observers' retinas, no matter where in the hallway they were located.

In the first part of Holway and Boring's experiment, many depth cues were available, including binocular disparity, motion parallax, and shading, so the observer could easily judge the distance of the test circles. The results, plotted in **Figure 10.35**, show that when the observers viewed a large test circle that was located far away (far circle in Figure 10.31), they made the comparison circle large (point F in Figure 10.35); when they viewed a small test circle that was located nearby (near circle in Figure 10.31), they made the comparison circle small (point N in Figure 10.35). Thus, when good depth cues were present, the observer's judgments of the size of the circles matched the physical sizes of the circles.

Holway and Boring then determined how eliminating depth information would affect the observer's judgments of size. They did this by having the observer view the test circles with one eye, which eliminated binocular disparity (line 2 in Figure 10.35); then by having the observer view the test circles through a peephole, which eliminated motion parallax (line 3); and finally by adding drapes to the hallway to eliminate shadows and reflections (line 4). Each time some depth information was eliminated, the observer's judgments of the sizes of the test circles became less accurate. When all depth information was eliminated, the observer's perception of size was determined not by the actual size of the test circles but by the relative sizes of the circle's images on the observer's retinas.

Because all of the test circles in Holway and Boring's experiment had the same retinal size, eliminating depth information caused them to be perceived as being about the same size. Thus, the results of this experiment indicate that size estimation is based on the actual sizes of objects when there is good depth information (blue lines), but that size estimation is strongly influenced by the object's visual angle when depth information is eliminated (red lines).

An example of size perception that is determined by visual angle is our perception of the sizes of the sun and the moon, which, by cosmic coincidence, have the same visual angle. The fact that they have identical visual angles becomes most obvious during an eclipse of the sun. Although we can see the flaming corona of the sun surrounding the moon, as shown in **Figure 10.36**, the moon's disk almost exactly covers the disk of the sun.

If we calculate the visual angles of the sun and the moon, the result is 0.5 degrees for both. As you can see in Figure 10.36, the moon is small (diameter 2,200 miles) but close (245,000 miles from Earth), whereas the sun is large (diameter 865,400 miles) but far away (93 million miles from Earth). Even though these two celestial bodies are vastly different in size, we perceive

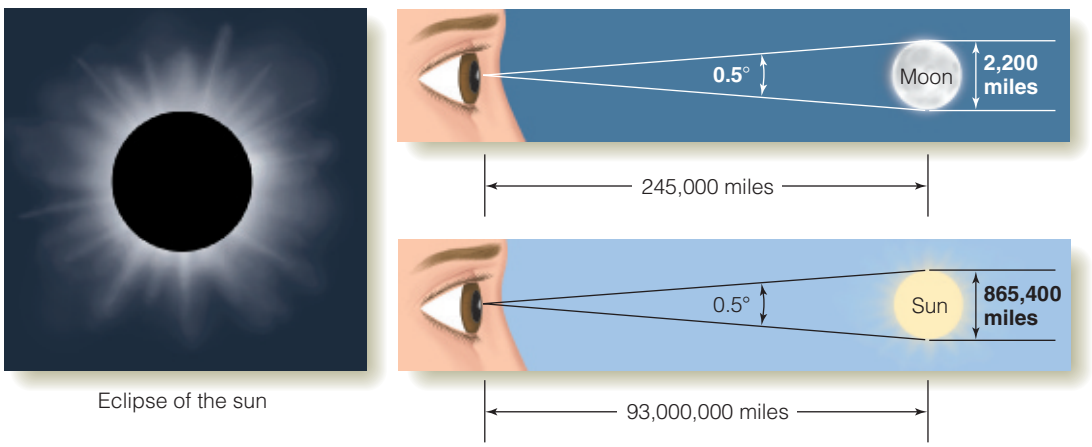

Figure 10.36 The moon's disk almost exactly covers the sun during an eclipse because the sun and the moon have the same visual angles.

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Bruce Goldstein

Figure 10.37 All of the palm trees appear to be the same size when viewed in the environment, even though the farther ones have a smaller visual angle.

them to be the same size because, as we are unable to perceive their distance, we base our judgment on their visual angles.

In yet another example, we perceive objects viewed from a high-flying airplane as very small. Because we have no way of accurately estimating the distance from the airplane to the ground, we perceive size based on objects' visual angles, which are very small because we are so high up.

Size Constancy

One of the most obvious features of the scene in **Figure 10.37**, on the campus of the University of Arizona, is that looking down the row of palm trees, each more distant tree becomes smaller in the picture. If you were standing on campus observing this scene, the more distant trees would appear to take up less of your field of view, as in the picture, but at the same time you would not perceive the farther tree as shorter than the near trees. Even though the far trees take up less of your field of view (or to put it another way, have a smaller *visual angle*), they appear constant in size. The fact that our perception of an object's size is relatively constant even when we view the object from different distances is called size constancy.

To introduce the idea of size constancy to my perception classes, I (BG) ask someone in the front row to estimate my height when I'm standing about 3 feet away. Their guess is usually accurate, around 5 feet 9 inches. I then take one large step back so I am now twice as far away and ask the person to estimate my height again. It probably doesn't surprise you that the second estimate of my heights is about the same as the first. The point of this demonstration is that even though my image on our students' retinas becomes half as large when I double my distance (compare Figures 10.32a and 10.32b), I do not appear to shrink to about 3 feet tall, but still appear to be my normal size. The following demonstration illustrates size constancy in another way.

DEMONSTRATION | Perceiving Size at a Distance

Hold a coin between the fingertips of each hand so you can see the faces of both coins. Hold one coin about a foot from you and the other at arm's length. Observe the coins with both of your eyes open and note their sizes. Under these conditions, most people perceive the near and far coins as being approximately the same size. Now close one eye, and holding the coins so they appear side-by-side, notice how your perception of the size of the far coin changes so that it now appears smaller than the near coin. This demonstrates how size constancy is decreased under conditions of poor depth information.

Although students often propose that size constancy works because we are familiar with the sizes of objects, research has shown that observers can accurately estimate the sizes of unfamiliar objects viewed at different distances (Haber & Levin, 2001).

Size Constancy as a Calculation The link between size constancy and depth perception has led to the proposal that size constancy is based on a mechanism called size–distance scaling that takes an object's distance into account (Gregory, 1966). Size–distance scaling operates according to the equation

$$S = K(R \times D)$$

where S is the object's perceived size, K is a constant, R is the size of the retinal image, and D is the perceived distance of the object. (Since we are mainly interested in R and D, and K is a scaling factor that is always the same, we will omit K in the rest of our discussion.)

According to the size–distance equation, as a person walks away from you, the size of the person's image on your retina (R) gets smaller, but your perception of the person's distance (D) gets larger. These two changes balance each other, and the net result is that you perceive the person's size (S) as staying the same.

DEMONSTRATION | Size–Distance Scaling and Emmert's Law

You can demonstrate size–distance scaling to yourself by illuminating the red circle in **Figure 10.38** with your desk lamp (or increase the brightness on your computer screen) and look at the + sign for about 60 seconds. Then look at the white space to the side of the circle. If you blink, you should see the circle's afterimage floating in front of the page. Before the afterimage fades, also look at a wall far across the room. You should see that the size of the afterimage depends on where you look. If you look at a distant surface, such as the far wall of the room, you see a large afterimage that appears to be far away. If you look at a near surface, such as a piece of paper, you see a small afterimage that appears to be close.

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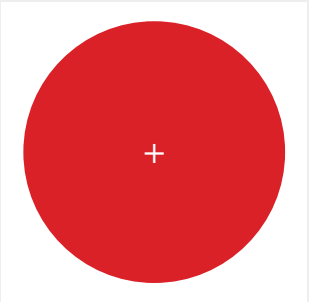

Figure 10.38 Look at the small + for 60 seconds.

Figure 10.39 illustrates the principle underlying the effect you just experienced, which was first described in 1881 by Emil Emmert (1844–1911). Staring at the square bleached a small circular area of visual pigment on your retina. This bleached area of the retina determined the retinal size of the afterimage and remained constant no matter where you were looking.

The perceived size of the afterimage, as shown in Figure 10.39, is determined by the distance of the surface against which the afterimage is viewed. This relationship between the apparent distance of an afterimage and its perceived size is known as Emmert's law: The farther away an afterimage appears, the larger it will seem. This result follows from our size–distance scaling equation, $S = R \times D$. The size of the bleached area of pigment on the retina (R) always stays the same, so that increasing the afterimage's distance (D) increases the magnitude of $R \times D$. We therefore perceive the size of the afterimage (S) as larger when it is viewed against the far wall.

The size–distance scaling effect demonstrated by the afterimage demonstration is working constantly when we look at objects in the environment, with the visual system taking both an object's size in the field of view (which determines retinal size) and its distance into account to determine our perception of its size. This process, which happens without any effort on our part, helps us perceive a stable environment. Just think of how confusing it would be if objects appeared to shrink or expand just because we happened to be viewing them from different distances. Luckily, because of size constancy, this doesn't happen.

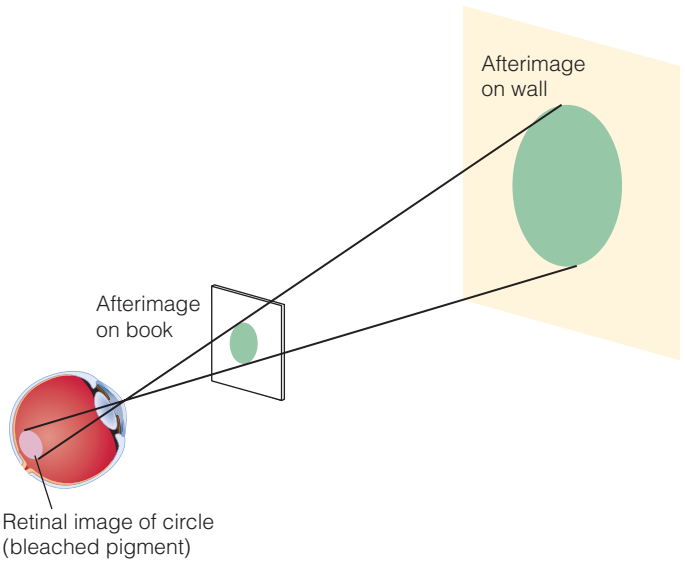

Figure 10.39 The principle behind the observation that the size of an afterimage increases as the afterimage is viewed against more distant surfaces.

Other Information for Size Perception Although we have been stressing the link between size constancy and depth perception and how size–distance scaling works, other sources of information in the environment also help us achieve size constancy. One source of information for size perception is relative size. We often use the sizes of familiar objects as a yardstick to judge the size of other objects. **Figure 10.40** shows two views of Henry Bruce's sculpture *The Giant's Chair*. In **Figure 10.40a**, it is difficult to determine how large the chair is; if you assume that the camera is positioned on the ground, you might think it looks to be a nice normal size for a chair. **Figure 10.40b**, however, leads us to a different conclusion. The presence of a man next to the chair indicates that the chair is extraordinarily large. This idea that our perception of the sizes of objects can be influenced by the sizes of nearby objects explains why we often fail to appreciate how tall basketball players are, when all we see for comparison are other basketball players. But as soon as a person of average height stands next to one of these players, the player's true height becomes evident.

Adam Burton/Getty Images

(a)

David Clapp/Getty Images

(b)

Figure 10.40 (a) The size of the chair is ambiguous until (b) a person is standing next to it.

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Bruce Goldstein

Figure 10.41 Two cylinders resting on a texture gradient. The fact that the bases of both cylinders cover the same number of units on the gradient indicates that the bases of the two cylinders are the same size.

Another source of information for size perception is the relationship between objects and texture information on the ground. We saw that a texture gradient occurs when elements that are equally spaced in a scene appear to be more closely packed as distance increases (Figure 10.8). **Figure 10.41** shows two cylinders sitting on a texture gradient formed by a cobblestone road. Even if we have trouble perceiving the depth of the near and far cylinders, we can tell that they are the same size because their bases both cover the same portion of a paving stone.

10.8 Illusions of Depth and Size

Visual illusions fascinate people because they demonstrate how our visual system can be "tricked" into seeing inaccurately (Bach & Poloschek, 2006). We have already described a number of types of illusions. Illusions of lightness include the Chevreul illusion (p. 58) and Mach bands (p. 59), in which small changes in lightness are seen near a border even though no changes are present in the physical pattern of light. Attentional effects include change blindness (p. 138), in which two alternating scenes appear similar even though there are differences between them. Illusions of motion are those in which stationary stimuli are perceived as moving (p. 179).

We will now describe some illusions of size—situations that lead us to misperceive the size of an object. We will see that the connection between the perception of size and the perception of depth has been used to explain some of these illusions. We begin with the Müller-Lyer illusion.

The Müller-Lyer Illusion

In the **Müller-Lyer illusion**, the right vertical line in **Figure 10.42** appears to be longer than the left vertical line, even though they are both exactly the same length (measure them). A number of different explanations have been proposed to explain this illusion. An influential early explanation involves size–distance scaling.

Misapplied Size Constancy Scaling Why does the Müller-Lyer display cause a misperception of size? Richard Gregory (1966) explains the illusion on the basis of a mechanism he calls **misapplied size constancy scaling**. He points out that size constancy normally helps us maintain a stable perception of objects by taking distance into account (as expressed in the size–distance scaling equation). Thus, size constancy scaling causes a 6-foot-tall person to appear 6 feet tall no matter what his distance. Gregory proposes, however, that the very mechanisms that help us maintain stable perceptions in the three-dimensional world sometimes create illusions when applied to objects drawn on a two-dimensional surface.

We can see how misapplied size constancy scaling works by comparing the left and right lines in Figure 10.42 to the left and right lines that have been superimposed on the corners in **Figure 10.43**. Both lines are the same size, but according to Gregory the lines appear to be at different distances because the fins on the right line in Figure 10.43 make this line look like part of an inside corner of a room, and the fins on the left line make this line look like part of a corner viewed from outside. Because inside corners appear to "recede" and outside corners "jut out," our size–distance scaling mechanism treats the inside corner as if it is farther away, so the term D in the equation $S = R \times D$ is larger and this line therefore appears longer. (Remember that the retinal sizes, R, of the two lines are the same, so perceived size, S, is determined by the perceived distance, D.)

At this point, you could say that although the Müller-Lyer figures may remind Gregory of inside and outside corners, they don't look that way to you (or at least they didn't until Gregory told you to see them that way). But according to Gregory, it is not necessary that you be consciously aware that these lines can represent three-dimensional structures; your perceptual system

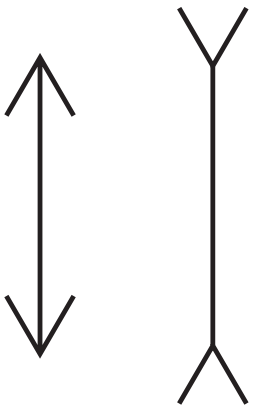

Figure 10.42 The Müller-Lyer illusion. Both lines are actually the same length.

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Figure 10.43 According to Gregory (1966), the Müller-Lyer line on the left corresponds to an outside corner, and the line on the right corresponds to an inside corner. Note that the two vertical lines are the same length (measure them!).

unconsciously takes the depth information contained in the Müller-Lyer figures into account, and your size–distance scaling mechanism adjusts the perceived sizes of the lines accordingly.

Gregory's theory of visual illusions has not, however, gone unchallenged. For example, figures like the dumbbells in **Figure 10.44**, which contain no obvious perspective or depth, still result in an illusion. And Patricia DeLucia and Julian Hochberg (1985, 1986, 1991; Hochberg, 1987) have shown that the Müller-Lyer illusion occurs for a three-dimensional display like the one in **Figure 10.45**. When viewed as a three-dimensional display, the distance between corners B and C appears to be greater than the distance between A and B, even though they are the same, and it is obvious that the spaces between the two sets of fins are not at different depths. You can experience this effect for yourself by doing the following demonstration.

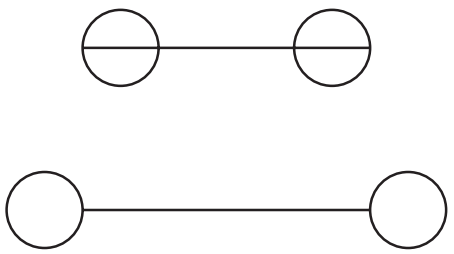

Figure 10.44 The "dumbbell" version of the Müller-Lyer illusion. As in the original Müller-Lyer illusion, the two straight lines are actually the same length.

DEMONSTRATION | **The Müller-Lyer Illusion With Books**

Pick three books that are the same size and arrange two of them with their corners making a 90-degree angle and standing in positions A and B, as shown in Figure 10.45. Then, without using a ruler, position the third book at position C, so that distance *x* appears to be equal to distance *y*. Check your placement, looking down at the books from the top and from other angles as well. When you are satisfied that distances *x* and *y* appear about equal, measure the distances with a ruler. How do they compare?

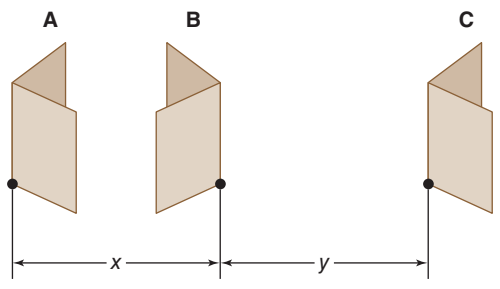

Figure 10.45 A three-dimensional Müller-Lyer illusion. The 2-foot-high wooden "fins" stand on the floor. Although the distances *x* and *y* are the same, distance *y* appears larger, just as in the two-dimensional Müller-Lyer illusion.

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If you set distance *y* so that it was smaller than distance *x*, this is exactly the result you would expect from the two-dimensional Müller-Lyer illusion, in which the distance between the outward-facing fins appears enlarged compared to the distance between the inward-facing fins. You can also duplicate the illusion shown in Figure 10.45 with your books by using your ruler to make distances *x* and *y* equal. Then, notice how the distances actually appear. The fact that we can create the Müller-Lyer illusion by using three-dimensional stimuli such as these, along with demonstrations like the dumbbell in Figure 10.44, is difficult for Gregory's theory to explain.

Conflicting Cues Theory R. H. Day (1989, 1990) has proposed the conflicting cues theory, which states that our perception of line length depends on two cues: (1) the actual length of the vertical lines and (2) the overall length of the figure. According to Day, these two conflicting cues are integrated to form a compromise perception of length. Because the overall length of the figure with outward-oriented fins is greater (Figure 10.42), the vertical line appears longer.

Another version of the Müller-Lyer illusion, shown in **Figure 10.46**, results in the perception that the space between the dots is greater in the lower figure than in the upper figure, even though the distances are actually the same. According to Day's conflicting cues theory, the space in the lower figure appears greater because the overall extent of the figure is greater. Notice that conflicting cues theory can also be applied to the dumbbell display in Figure 10.44. Thus, although Gregory believes that depth information is involved in determining illusions, Day rejects this idea and proposes that cues for length are what is important. Let's now look at some more examples of illusions and the mechanisms that have been proposed to explain them.

The Ponzo Illusion

In the Ponzo (or railroad track) illusion, shown in **Figure 10.47**, both animals are the same size on the page, and so have the same visual angle, but the one on top appears longer. According to Gregory's misapplied scaling explanation, the top animal appears bigger because of depth information provided by the converging railroad tracks that make the top animal appear farther away. Thus, just as in the Müller-Lyer illusion, the scaling mechanism corrects for this apparently increased depth (even though there really isn't any, because the illusion is on a flat page), and we perceive the top animal to be larger. (Also see Prinzmetal et al., 2001, and Shimamura & Prinzmetal, 1999, for another explanation of the Ponzo illusion.)

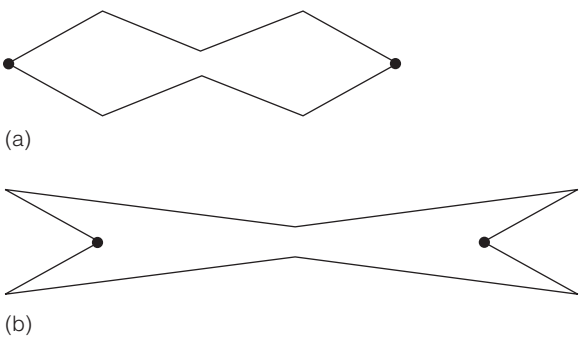

Figure 10.46 An alternate version of the Müller-Lyer illusion. We perceive that the distance between the dots in (a) is less than the distance in (b), even though the distances are the same. (From Day, 1989)

William Vann/www.edupic.net

Figure 10.47 The Ponzo (or railroad track) illusion. The two animals are the same length on the page (measure them), but the far one appears larger.

The Ames Room

The Ames room causes two people of equal size to appear very different in size (Ittelson, 1952). In **Figure 10.48a**, you can see that the woman on the left looks much taller than the man on the right, but when they change sides, in **Figure 10.48b**, the man appears much larger than the woman. This perception occurs even though both people are actually about the same height. The reason for this erroneous perception of size lies in the construction of the room. The shapes of the wall and the windows at the rear of the room make it look like a normal rectangular room when viewed from a particular observation point; however, as shown in the diagram in **Figure 10.49**, the Ames room is actually shaped so that the right corner of the room is almost twice as far from the observer as the left corner.

What's happening in the Ames room? The construction of the room causes the person on the right to have a much smaller visual angles than the person on the left. We think that we are looking into a normal rectangular room at two people who appear to be at the same distance, so we perceive the one with the smaller visual angle as shorter. We can understand why

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(a)

(b)

STEPHANIE PILICK/Getty Images

Figure 10.48 The Ames room. Although the man and woman are about the same height, (a) the woman appears taller or (b) the man appears taller because of the distorted shape of the room.

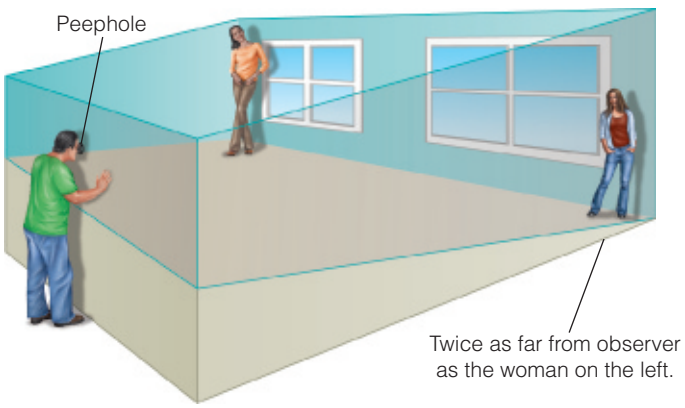

Figure 10.49 The Ames room, showing its true shape. The person on the right is actually almost twice as far away from the observer as the person on the left; however, when the room is viewed through the peephole, this difference in distance is not seen. In order for the room to look normal when viewed through the peephole, it is necessary to enlarge the right side of the room.

this occurs by returning to our size–distance scaling equation, $S = R \times D$. Because the *perceived* distance (D) is the same for the two people, but the size of the retinal image (R) is smaller for the people on the right, their perceived size (S) is smaller.

Another explanation for the Ames room is based not on size–distance scaling but on relative size. The relative size explanation states that our perception of the size of the two people is determined by how they fill the distance between the bottom and top of the room. Because the person on the left fills the entire space and the person on the right occupies only a little of it, we perceive the person on the left as taller (Sedgwick, 2001).

SOMETHING TO CONSIDER:

The Changing Moon

Every so often the moon makes the news. "A supermoon is going to happen," it is proclaimed, because the moon is going to be closer than usual to the earth. This closeness, which is caused by the moon's slightly elliptical orbit, is claimed to make the supermoon appear larger than usual. In reality, however, the supermoon is only about 14 percent larger than normal, an effect that falls far short of "super," and which most people wouldn't even notice if they hadn't heard about it in the news.

The best way to perceive the moon as larger, it turns out, is not to rely on a slight change in the moon's distance, but to rely on your mind. You have probably noticed that when the moon is on the horizon it appears much larger than when it is high in the sky, an effect called the moon illusion (**Figure 10.50**).

We say that this effect is caused by your mind, because the visual angles of the horizon moon and the elevated moon are

Figure 10.50 An artist's conception of the how the moon is perceived when it is on the horizon and when it is high in the sky. Note that the visual angle of the horizon moon is depicted as larger than the visual angle of the moon high in the sky. This is because the picture is simulating the illusion. In the environment, the visual angles of the two moons are the same.

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J.Lopez Photography/Shutterstock

Rising moon over LA

Figure 10.51 Time-lapse photograph showing that the moon's visual angle remains constant as it rises above the horizon.

the same. This must be so because the moon's physical size (2,200 miles in diameter) stays the same and it remains the same distance from Earth (245,000 miles) throughout the night. This constancy of the moon's visual angle is shown in **Figure 10.51**, which is a time-lapse photograph of the moon rising. The camera, which is not susceptible to the moon illusion, just records the size of the moon's image in the sky. You can demonstrate this constancy to yourself by viewing the moon when it is on the horizon and when it is high in the sky through a quarter-inch-diameter hole held at about arm's length. For most people, the moon just fits inside this hole, wherever it is in the sky.

What causes the mind to enlarge the horizon moon? According to **apparent distance theory**, the answer has to do with the perceived distance of the moon. The moon on the horizon appears more distant because it is viewed across the filled space of the terrain, which contains depth information. However, when the moon is higher in the sky, it appears less distant because it is viewed through empty space, which contains little depth information. The idea that the horizon is perceived as farther away than the sky overhead is supported by the fact that when people estimate the distance to the horizon and the distance to the sky directly overhead, they report that the horizon appears to be farther away. That is, the heavens appear "flattened" (**Figure 10.52**).

The key to the moon illusion, according to apparent distance theory, is the size–distance scaling equation, $S = R \times D$. Retinal size, R, is the same for both locations of the moon (since the visual angle is always the same no matter where the moon appears in the sky), but D is greater when the moon is on the horizon, so it appears larger (Kaufman & Kaufman, 2000). This is the principle we invoked in the Emmert's law demonstration to explain why the afterimage appears larger when it is viewed against a faraway surface (King & Gruber, 1962).

Lloyd Kaufman and Irvin Rock (1962a, 1962b) did a number of experiments that support the apparent distance theory. In one of their experiments, they showed that when the horizon moon was viewed over the terrain, which made it seem farther away, it appeared 1.3 times larger than the elevated moon; however, when the terrain was masked off so that the horizon moon was viewed through a hole in a sheet of cardboard, the illusion vanished.

Some researchers, however, question the idea that the horizon moon appears farther, as shown in the flattened heavens effect in Figure 10.52, because some observers see the horizon moon as floating in space in front of the sky (Plug & Ross, 1994).

Another theory of the moon illusion, the **angular size contrast theory**, proposes that the high in the sky moon appears smaller because the large expanse of sky surrounding it makes it appear smaller by comparison. However, when the moon is on the horizon, less sky surrounds it, so it appears larger (Baird et al., 1990).

Even though scientists have been proposing theories to explain the moon illusion for hundreds of years, there is still no agreement on an explanation (Hershenson, 1989). Apparently a number of factors are involved, in addition to the ones we have considered here, including atmospheric perspective (looking through haze on the horizon can increase size perception), color (redness increases perceived size), and oculomotor factors (convergence of the eyes, which tends to occur when we look toward the horizon and can cause an increase in perceived size; Plug & Ross, 1994). Just as many different sources of depth information work together to create our impression of depth, many different factors may work together to create the moon illusion, and perhaps the other illusions as well.

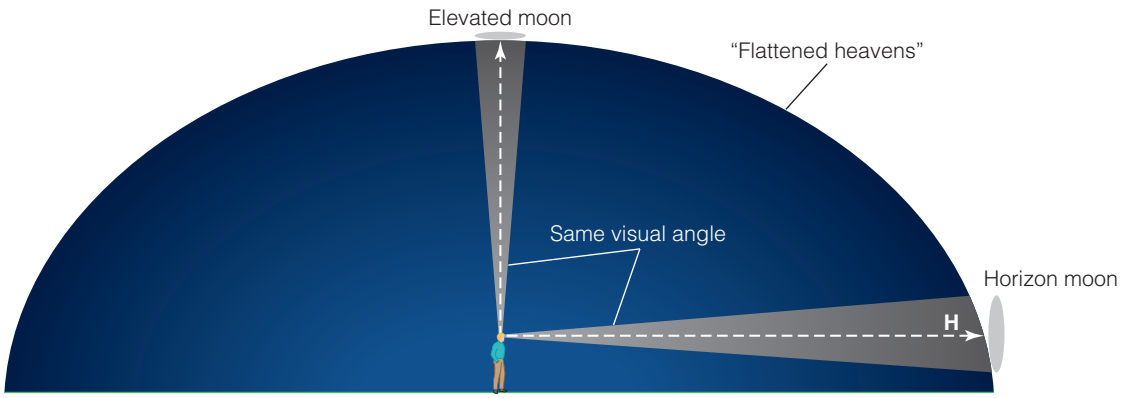

Figure 10.52 When observers are asked to consider the sky as a surface and to compare the distance to the horizon (H) and the distance to the top of the sky on a clear moonless night, they usually say that the horizon appears farther away. This results in the "flattened heavens" shown here.

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At what age are infants able to use different kinds of depth information?

A 3-day-old infant, sitting in a specially designed baby seat in a dark room, sees an optic flow stimulus (see Chapter 7, page 150) made up of dots moving on monitors placed on either side of the infant's head. When the flow is moving from front to back, like what happens when moving forward in depth (see Figure 7.3a), the infant's head pushes backward, with more pressure for higher rates of flow. Thus, 3-day-old infants are sensitive to optic flow (Jouen et al., 2000). And at the age of 3 weeks, infants blink in response to a stimulus that appears to be moving toward their face (Nanez, 1988). Both of these observations indicate that behaviors related to depth are present in infants less than a month old.

But what about the kinds of depth information we have described in this chapter? Different types of information become operative at different times. We first consider binocular disparity, which becomes effective between 3 and 6 months of age, and then pictorial depth cues, which become effective slightly later, between 4 and 7 months.

Binocular Disparity

One requirement for the operation of binocular disparity is that the eyes must be able to **binocularly fixate**, so that the two eyes are both looking directly at the object and the two foveas are directed to exactly the same place. Newborns have only a rudimentary, imprecise ability to fixate binocularly, especially on objects that are changing in depth (Slater & Findlay, 1975).

Richard Aslin (1977) determined when binocular fixation develops by making some simple observations. He filmed infants' eyes while he moved a target back and forth between 12 cm and 57 cm from the infant. When the infant is directing both eyes at a target, the eyes should diverge (rotate outward) as the target moves away and should converge (rotate inward) as the target moves closer. Aslin's films indicate that although some divergence and convergence do occur in 1- and 2-month-old infants, these eye movements do not reliably direct both eyes toward the target until about 3 months of age.

Although binocular fixation may be present by 3 months of age, this does not guarantee that the infant can use the resulting disparity information to perceive depth. To determine when infants can use this information to perceive depth, Robert Fox and coworkers (1980) presented random-dot stereograms to infants ranging in age from 2 to 6 months (see page 241 to review random-dot stereograms).

The beauty of random-dot stereograms is that the binocular disparity information in the stereograms results in stereopsis. This occurs only (1) if the stereogram is observed with a device that presents one picture to the left eye and the other picture to the right eye, and (2) if the observer's visual system can convert this disparity information into the perception of depth. Thus, if we present a random-dot stereogram to an infant whose visual system cannot yet use disparity information, all he or she sees is a random collection of dots.

In Fox's experiment, an infant wearing special viewing glasses was seated in his or her mother's lap in front of a television screen (**Figure 10.53**). The child viewed a random-dot stereogram that appeared, to an observer sensitive to disparity information, as a rectangle-in-depth, moving either to the left or to the right. Fox's premise was that an infant sensitive to disparity will move his or her eyes to follow the moving rectangle. He found that infants younger than about 3 months of age would not follow the rectangle, but that infants between 3 and 6 months of age would follow it. He therefore concluded that the ability to use disparity information to perceive depth emerges sometime between 3½ and 6 months of age. This time for the emergence of binocular depth perception has been confirmed by other research using a variety of different methods (Held et al., 1980; Shimojo et al., 1986; Teller, 1997).

Pictorial Cues

Another type of depth information is provided by pictorial cues. These cues develop later than disparity, presumably because they depend on experience with the environment and the development of cognitive capabilities. In general, infants begin to use pictorial cues such as overlap, familiar size, relative size, shading, linear perspective, and texture gradients sometime between about 4 and 7 months of age (Kavšek et al., 2009; Shuwairi & Johnson, 2013; Yonas et al., 1982). We will describe research on two of these cues: familiar size and cast shadows.

Depth From Familiar Size Granrud and coworkers (1985) conducted a two-part experiment to see whether infants

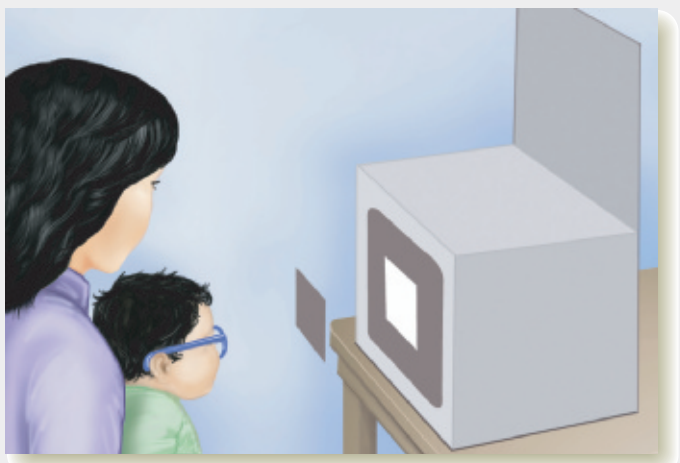

Figure 10.53 The setup used by Fox et al. (1980) to test infants' ability to use binocular disparity information. If the infant can use disparity information to see depth, he or she sees a rectangle moving back and forth in front of the screen. (From Shea et al., 1980)

Continued

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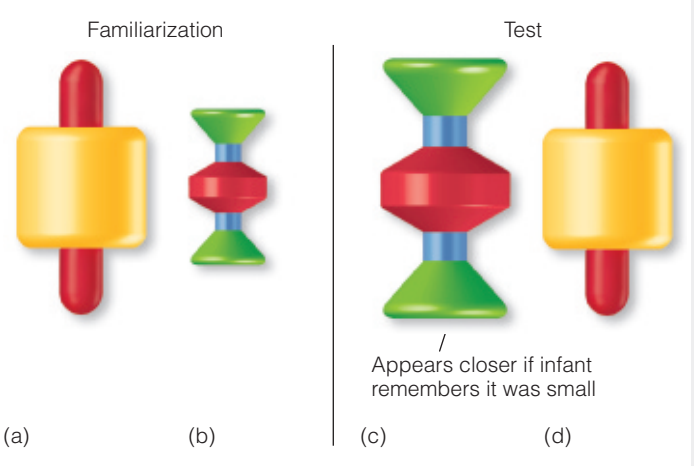

Figure 10.54 Stimuli for Granrud et al.'s (1985) familiar size experiment. See text for details. (From Granrud et al., 1985)

can use their knowledge of the sizes of objects to help them perceive depth. In the *familiarization period*, 5- and 7-month-old infants played with a pair of wooden objects for 10 minutes. One of these objects was large (**Figure 10.54a**), and one was small (**Figure 10.54b**). In the *test period*, about a minute after the familiarization period, objects (c) and (d) were the same size and were presented at the same distance from the infant. The prediction was that infants sensitive to familiar size would perceive the object at (c) to be closer if they remembered, from the familiarization period, that this shape was smaller than the other one. If the infant remembered the green object as being small, then seeing it as big in their field of view could lead the infant to think it was the same small object, but located much closer. How can we determine whether an infant perceives one object as closer than another? The most widely used method is observing an infant's reaching behavior.

METHOD | Preferential Reaching

The preferential reaching procedure is based on observations that infants as young as 2 months old will reach for nearby objects and that 5-month-old infants are extremely likely to reach for an object that is placed within their reach and unlikely to reach for an object that is beyond their reach (Yonas & Hartman, 1993). Infants' sensitivity to depth has therefore been measured by presenting two objects side by side. As with the preferential looking procedure (Chapter 3, page 60), the left–right position of the objects is changed across trials. The ability to perceive depth is inferred when the infant consistently reaches more for the object that contains information indicating it is closer. When a real depth difference is presented, infants use binocular information and reach for the closer object almost 100 percent of the time. To test infants' use of pictorial depth information only, an eye patch is placed on one eye (this eliminates the availability of binocular information, which overrides pictorial depth cues). If infants are sensitive to the pictorial depth information, they reach for the apparently closer object approximately 60 percent of the time.

When Granrud and coworkers presented the objects to infants, 7-month-olds reached for object (c), as would be predicted if they perceived it as being closer than object (d). The 5-month-olds, however, did not reach for object (c), which indicated that these infants did not use familiar size as information for depth. Thus, the ability to use familiar size to perceive depth appears to develop sometime between 5 and 7 months.

This experiment is interesting not only because it indicates when the ability to use familiar size develops, but also because the infant's response in the test phase depends on a cognitive ability—the ability to remember the sizes of the objects that he or she played with in the familiarization phase. The 7-month-old infant's depth response in this situation is therefore based on both what is perceived and what is remembered.

Depth From Cast Shadows We know that shadows provide information indicating an object's position relative to a surface, as occurred in Figure 10.9 (p. 233). To determine when this ability is present in infants, Albert Yonas and Carl Granrud (2006) presented 5- and 7-month-old infants with a display like the one in **Figure 10.55**. Adults and older children consistently report that the object on the right appears nearer than the object on the left. When the infants viewed this display monocularly (to eliminate binocular depth information that would indicate that the objects were actually flat), the 5-month-old infants reached for both the right and left objects on 50 percent of the trials, indicating no preference for the right object. However, the 7-month-old infants reached for the right object on 59 percent of the trials. Yonas and Granrud concluded from this result that 7-month-old infants perceive depth information provided by cast shadows.

This finding fits with other research that indicates that sensitivity to pictorial depth cues develops between 5 and 7 months (Kausek et al., 2009). But what makes these results especially interesting is that they imply that the infants were able to tell that the dark areas under the toy were shadows

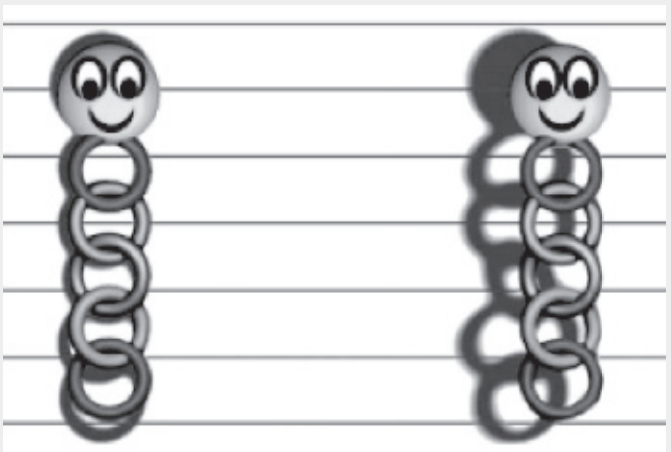

Figure 10.55 Stimuli presented to 7-month-old children in Granrud et al.'s (1985) familiar size experiment: Left: familiarization stimulus; Right: test stimulus.

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and not dark markings on the wall. It is likely that this ability, like the other pictorial depth cues, is based largely on learning from interacting with objects in the environment. In this case, infants need to know something about shadows, including an understanding that most light comes from above (see page 105).

The research we have described shows that infant depth perception develops during the first year of life, beginning with involuntary responses to motion and potentially threatening stimuli in the first weeks, to binocular disparity at 3 to 6 months and pictorial depth cues at 4 to 7 months. As impressive as this early development is, it is also important to realize that it takes many years, stretching into late childhood, before the different sources of depth information become coordinated and integrated with each other to achieve the adult experience of depth perception (Nardini et al., 2010).

TEST YOURSELF 10.2

1. Describe the Holway and Boring experiment. What do the results of this experiment tell us about how size perception is influenced by depth perception?
2. What are some examples of situations in which our perception of an object's size is determined by the object's visual angle? Under what conditions does this occur?
3. What is size constancy, and under what conditions does it occur?
4. What is size–distance scaling? How does it explain size constancy?
5. Describe two types of information (other than depth) that can influence our perception of size.
6. Describe how illusions of size, such as the Müller-Lyer illusion, the Ponzo illusion, the Ames room, and the moon illusion, can be explained in terms of size–distance scaling.
7. What are some problems with the size–distance scaling explanation of (a) the Müller-Lyer illusion and (b) the moon illusion? What alternative explanations have been proposed?
8. What is the evidence that infants have some responses to depth-related stimuli in the first month of life?
9. Describe experiments that showed when infants can perceive depth using binocular disparity and using pictorial (monocular) cues. Which develops first? What methods were used?

THINK ABOUT IT

1. One of the triumphs of art is creating the impression of depth on a two-dimensional canvas. Go to a museum or look at pictures in an art book, and identify the depth information that helps increase the perception of depth in these pictures. You may also notice that you perceive less depth in some pictures, especially abstract ones. In fact, some artists purposely create pictures that are perceived as "flat." What steps do these artists have to take to accomplish this? (p. 231)
2. Texture gradients are said to provide information for depth perception because elements in a scene become more densely packed as distance increases. The examples of texture gradients in Figures 10.6 and 10.8 contain regularly spaced elements that extend over large distances. But regularly spaced elements are more the exception than the rule in the environment. Make an informal survey of your environment, both inside and outside, and decide (a) whether texture gradients are present in your environment and (b) if you think the principle behind texture gradients could contribute to the perception of depth even if the texture information in the environment is not as obvious as in the examples in this chapter. (p. 233)
3. How could you determine the contribution of binocular vision to depth perception? One way would be to close one eye and notice how this affects your perception. Try this, and describe any changes you notice. Then devise a way to quantitatively measure the accuracy of depth perception that is possible with two-eyed and one-eyed vision. (p. 249)

KEY TERMS

Absolute disparity (p. 239)
Accommodation (p. 231)
Accretion (p. 234)
Ames room (p. 254)
Angle of disparity (p. 239)
Angular size contrast theory (p. 256)
Apparent distance theory (p. 256)
Atmospheric perspective (p. 233)
Binocular depth cell (p. 243)
Binocular disparity (p. 238)
Binocularly fixate (p. 257)
Conflicting cues theory (p. 254)
Convergence (p. 231)
Correspondence problem (p. 242)
Corresponding retinal points (p. 238)

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Crossed disparity (p. 240)
Cue approach to depth perception (p. 230)
Deletion (p. 234)
Disparity-selective cell (p. 243)
Disparity tuning curve (p. 243)
Echolocation (p. 246)
Emmert's law (p. 251)
Familiar size (p. 231)
Frontal eyes (p. 244)
Horopter (p. 239)
Lateral eyes (p. 245)
Misapplied size constancy scaling (p. 252)
Monocular cue (p. 231)
Moon illusion (p. 255)
Motion parallax (p. 234)
Müller-Lyer illusion (p. 252)
Noncorresponding points (p. 239)
Occlusion (p. 230)
Oculomotor cue (p. 231)
Perspective convergence (p. 232)
Pictorial cue (p. 231)
Ponzo illusion (p. 254)
Random-dot stereogram (p. 240)
Relative disparity (p. 240)
Relative height (p. 231)
Relative size (p. 232)
Size constancy (p. 250)
Size–distance scaling (p. 196)
Stereopsis (p. 240)
Stereoscope (p. 241)
Stereoscopic depth perception (p. 236)
Stereoscopic vision (p. 236)
Strabismus (p. 236)
Texture gradient (p. 233)
Uncrossed disparity (p. 240)
Visual angle (p. 247)

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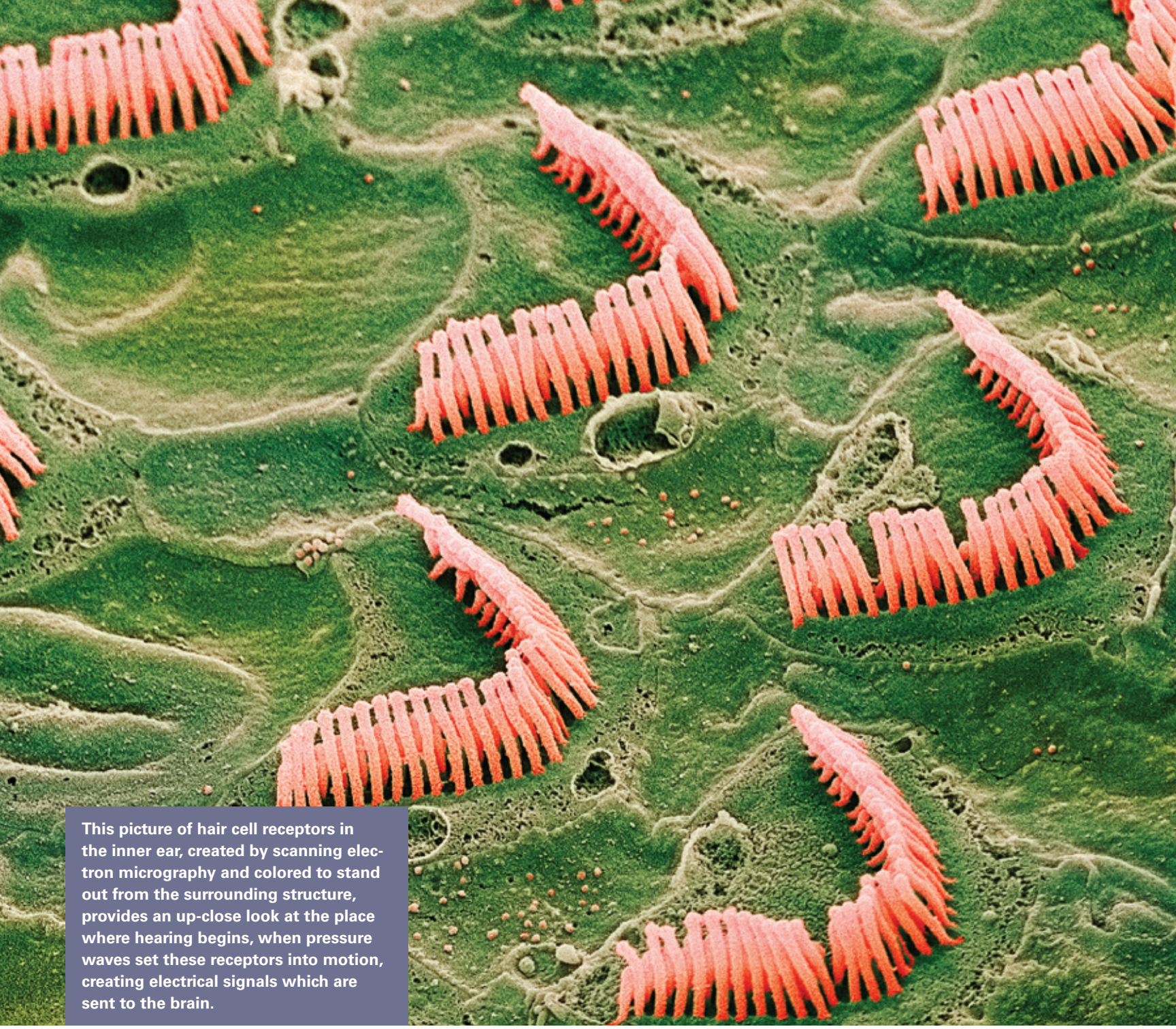

This picture of hair cell receptors in the inner ear, created by scanning electron micrography and colored to stand out from the surrounding structure, provides an up-close look at the place where hearing begins, when pressure waves set these receptors into motion, creating electrical signals which are sent to the brain.

SPL/Science Source

Learning Objectives

After studying this chapter, you will be able to ...

- Describe the physical aspects of sound, including sound waves, tones, sound pressure, and sound frequencies.
- Describe the perceptual aspects of sound, including thresholds, loudness, pitch, and timbre.
- Identify the basic structures of the ear and describe how sound acts on these structures to cause electrical signals.
- Describe how different frequencies of sound vibrations are translated into neural activity in the auditory nerve.
- Understand evidence supporting the idea that perceiving a tone's pitch depends on both *where* vibrations occur in the inner ear and on the *timing* of these vibrations.
- Describe what happens as nerve impulses travel along the pathway that leads from the ear to the cortex, and how pitch is represented in the cortex.
- Describe some of the mechanisms responsible for hearing loss.
- Describe procedures that have been used to measure infants' thresholds for hearing and their ability to recognize their mother's voice.

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CHAPTER 11

Hearing

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THINK ABOUT IT

Some Questions We Will Consider:

- If a tree falls in the forest and no one is there to hear it, is there a sound? (p. 264)
- How do sound vibrations inside the ear lead to the perception of different pitches? (p. 280)
- How can sound damage the auditory receptors? (p. 284)

Jill Robbins, a student in my class, wrote the following about the importance of hearing in her life:

> Hearing has an extremely important function in my life. I was born legally blind, so although I can see, my vision is highly impaired and is not correctable. Even though I am not usually shy or embarrassed, sometimes I do not want to call attention to myself and my disability.... There are many methods that I can use to improve my sight in class, like sitting close to the board or copying from a friend, but sometimes these things are impossible. Then I use my hearing to take notes.... My hearing is very strong. While I do not need my hearing to identify people who are very close to me, it is definitely necessary when someone is calling my name from a distance. I can recognize their voice, even if I cannot see them.

Hearing is extremely important to Jill because of her reduced vision. But even people with clear vision depend on hearing more than they may realize. Unlike vision, which depends on light traveling from objects to the eye, sound travels around corners to make us aware of events that otherwise would be invisible. For example, in my office in the psychology department, I hear things that I would be unaware of if I had to rely only on my sense of vision: people talking in the hall; a car passing by on the street below; an ambulance, siren blaring, heading up the hill toward the hospital. If it weren't for hearing, my world at this particular moment would be limited to what I can see in my office and the scene directly outside my window. Although the silence might make it easier to concentrate on writing this book, without hearing I would be unaware of many of the events in my environment.

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Our ability to hear events that we can't see serves an important signaling function for both animals and humans. For an animal living in the forest, the rustle of leaves or the snap of a twig may signal the approach of a predator. For humans, hearing provides signals such as the warning sound of a smoke alarm or an ambulance siren, the distinctive high-pitched cry of a baby who is distressed, or telltale noises that indicate problems in a car engine. Hearing not only informs us about things that are happening that we can't see, but perhaps most important of all, it adds richness to our lives through music and facilitates communication by means of speech.

This chapter is the first of four chapters on hearing. We begin, as we did for vision, by asking some basic questions about the stimulus: How can we describe the pressure changes in the air that is the stimulus for hearing? How is the stimulus measured? What perceptions does it cause? We then describe the anatomy of the ear and how the pressure changes make their way through the structures of the ear in order to stimulate the receptors for hearing.

Once we have established these basic facts about auditory system stimulus and structure, we consider one of the central questions of auditory research: What is the physiological mechanism for our perception of pitch, which is the quality that orders notes on a musical scale, as when we go from low to high pitches by moving from left to right on a piano keyboard? We will see that the search for the physiological mechanism of pitch has led to a number of different theories and that, although we understand a great deal about how the auditory system creates pitch, there are still problems that remain to be solved.

Near the end of this chapter, we complete our description of the structure of the auditory system by describing the pathway from the ear to the auditory cortex. This sets the stage for the next three chapters, in which we will expand our horizons beyond pitch to consider how hearing occurs in the natural environment, which contains many sound sources (Chapter 12), and also what mechanisms are responsible for our ability to perceive complex stimuli like music (Chapter 13) and speech (Chapter 14). The starting point for all of this is the perceptual process that we introduced in Chapter 1, which begins with the distal stimulus—the stimulus in the environment.

The distal stimulus for vision, in our example in Figure 1.4 (page 7), was a tree, which our observer was able to see because light was reflected from the tree into the eye. Information about the tree, transmitted by the light, then created a representation of the tree on the visual receptors.

But what happens when a bird, perched on the tree, sings? The back and forth action of the bird's vocal organ is transformed into a sound stimulus—pressure changes in the air. These pressure changes trigger a sequence of events that results in a representation of the bird's song within the ears, the sending of neural signals to the brain, and our eventual perception of the bird's song.

We will see that sound stimuli can be simple repeating pressure changes, like those often used in laboratory research, or more complex pressure changes such as those produced by our singing bird, musical instruments, or a person talking. The properties of these air pressure changes determine our ability to hear and are translated into sound qualities such as soft or loud, low-pitched or high-pitched, mellow or harsh. We begin by describing sound stimuli and their effects.

11.1 Physical Aspects of Sound

The first step in understanding hearing is to define what we mean by *sound* and to describe the characteristics of sound. One way to answer the question "What is sound?" is to consider the following question: *If a tree falls in the forest and no one is there to hear it, is there a sound?*

This question is useful because it shows that we can use the word **sound** both as a physical stimulus and as a perceptual response. The answer to the question about the tree depends on which of the following definitions of sound we use.

- Physical definition: Sound is *pressure changes* in the air or other medium.
- Perceptual definition: Sound is the *experience* we have when we hear.

The answer to the question "Is there a sound?" is "yes" if we are using the physical definition, because the falling tree causes pressure changes whether or not someone is there to hear them. The answer to the question is "no" if we are using the perceptual definition, because if no one is in the forest, there will be no experience.

This difference between physical and perceptual is important to be aware of as we discuss hearing in this chapter and the next three (also see page 268). Luckily, it is usually easy to tell from the context in which the terms are used whether "sound" refers to the physical stimulus or to the experience of hearing. For example, "the piercing sound of the trumpet filled the room" refers to the *experience of sound*, but "the sound had a frequency of 1,000 Hz" refers to sound as a *physical stimulus*. In general, we will use the term "sound" or "sound stimulus" to refer to the physical stimulus and "sound perception" to refer to the experience of sound. We begin by describing sound as a physical stimulus.

Sound as Pressure Changes

A sound stimulus occurs when the movements or vibrations of an object cause pressure changes in air, water, or any other elastic medium that can transmit vibrations. Let's begin by considering a loudspeaker, which is really a device for producing vibrations to be transmitted to the surrounding air. In extreme cases, such as standing near a speaker at a rock concert, these vibrations can be felt, but even at lower levels, the vibrations are there.

The speaker's vibrations affect the surrounding air, as shown in **Figure 11.1a**. When the diaphragm of the speaker

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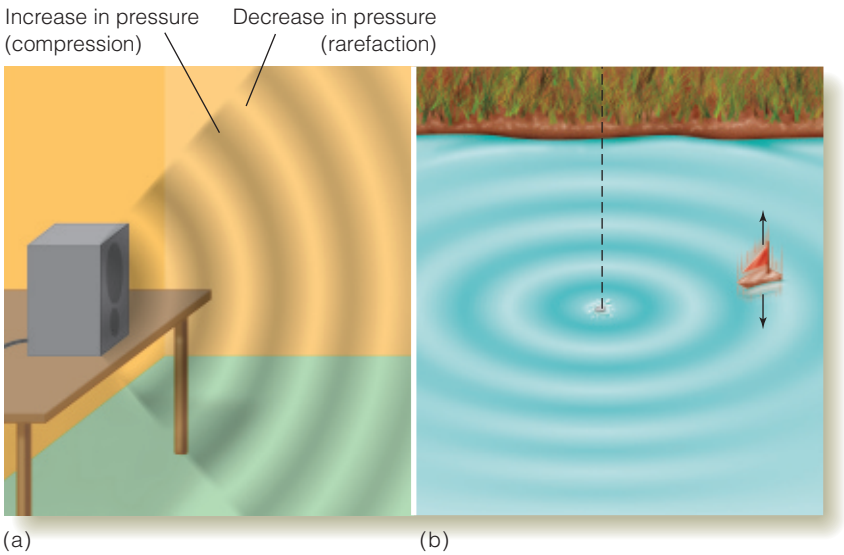

Figure 11.1 (a) The effect of a vibrating speaker diaphragm on the surrounding air. Dark areas represent regions of high air pressure, and light areas represent areas of low air pressure. (b) When a pebble is dropped into still water, the resulting ripples appear to move outward. However, the water is actually moving up and down, as indicated by movement of the boat. A similar situation exists for the sound waves produced by the speaker in (a).

moves out, it pushes the surrounding air molecules together, a process called *compression*, which causes a slight increase in the density of molecules near the diaphragm. This increased density results in a local increase in the air pressure above atmospheric pressure. When the speaker diaphragm moves back in, air molecules spread out to fill in the increased space, a process called *rarefaction*. The decreased density of air molecules caused by rarefaction causes a slight decrease in air pressure. By repeating this process hundreds or thousands of times a second, the speaker creates a pattern of alternating high- and low-pressure regions in the air, as neighboring air molecules affect each other. This pattern of air pressure changes, which travels through air at 340 meters per second (and through water at 1,500 meters per second), is called a **sound wave**.

You might get the impression from Figure 11.1a that this traveling sound wave causes air to move outward from the speaker into the environment. However, although *air pressure changes* move outward from the speaker, the *air molecules* at each location move back and forth but stay in about the same place. What is transmitted is the pattern of increases and decreases in pressure that eventually reach the listener's ear. What is actually happening is analogous to the ripples created by a pebble dropped into a still pool of water (**Figure 11.1b**). As the ripples move outward from the pebble, the water at any particular place moves up and down. The fact that the water does not move forward becomes obvious when you realize that the ripples would cause a toy boat to bob up and down—not to move outward.

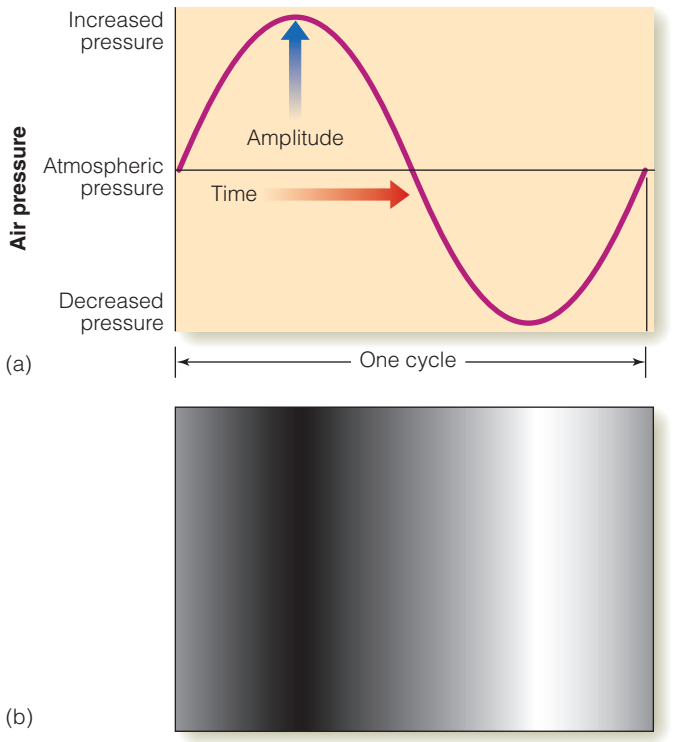

Figure 11.2 (a) Plot of sine-wave pressure changes for a pure tone. (b) Pressure changes are indicated, as in Figure 11.1, by darkening (pressure increased relative to atmospheric pressure) and lightening (pressure decreased relative to atmospheric pressure).

Pure Tones

To describe the pressure changes associated with sound, we will first focus on a simple kind of sound wave called a pure tone. A **pure tone** occurs when changes in air pressure occur in a pattern described by a mathematical function called a *sine wave*, as shown in **Figure 11.2**. Tones with this pattern of pressure changes are occasionally found in the environment. A person whistling or the high-pitched notes produced by a flute are close to pure tones. Tuning forks, which are designed to vibrate with a sine-wave motion, also produce pure tones. For laboratory studies of hearing, computers generate pure tones that cause a speaker diaphragm to vibrate in and out with a sine-wave motion. This vibration can be described by noting its **frequency**—the number of cycles per second that the pressure changes repeat—and its **amplitude**—the size of the pressure change.

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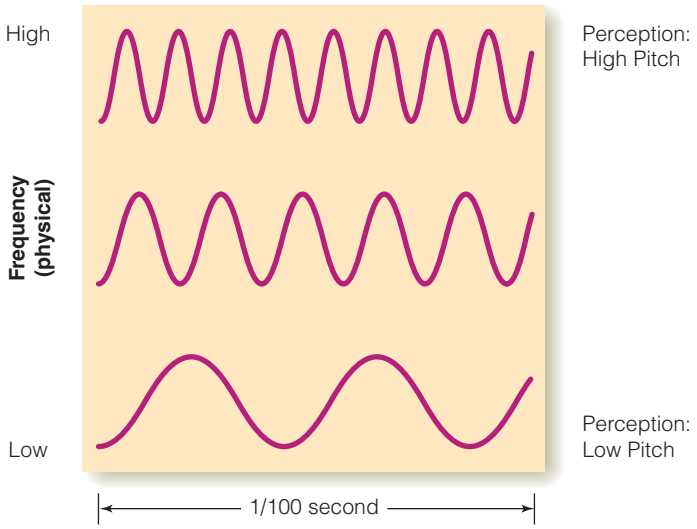

Figure 11.3 Three different frequencies of a pure tone. Higher frequencies are associated with the perception of higher pitches.

Sound Frequency Frequency, the number of cycles per second that the change in pressure repeats, is measured in units called Hertz (Hz), in which 1 Hz is 1 cycle per second. **Figure 11.3** shows pressure changes for three frequencies, ranging from high (top) to low (bottom). The middle stimulus in Figure 11.3, which repeats five times in 1/100 second, is a 500-Hz tone. As we will see, humans can perceive frequencies ranging from about 20 Hz to about 20,000 Hz, with higher frequencies usually being associated with higher pitches.

Sound Amplitude and the Decibel Scale One way to specify a sound's amplitude would be to indicate the difference in pressure between the high and low peaks of the sound wave. **Figure 11.4** shows three pure tones with different amplitudes.

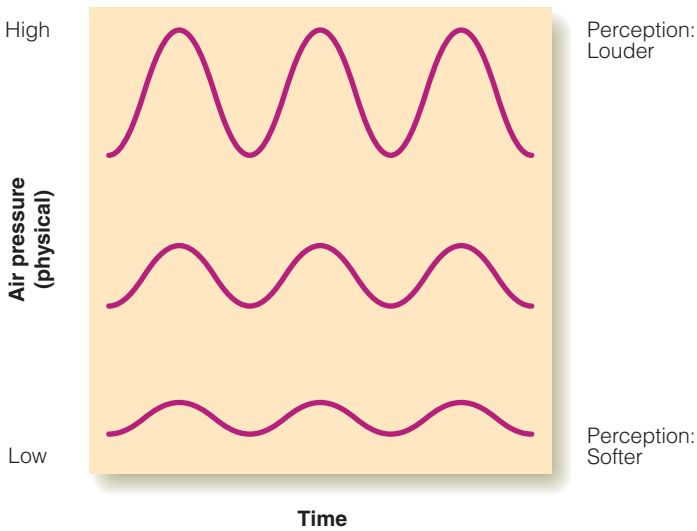

Figure 11.4 Three different amplitudes of a pure tone. Larger amplitude is associated with the perception of greater loudness.

Table 11.1 Relative Amplitudes and Decibels for Environmental Sounds

SOUND	RELATIVE AMPLITUDE	DECIBELS (DB)
Barely audible (threshold)	1	0
Leaves rustling	10	20
Quiet residential community	100	40
Average speaking voice	1,000	60
Express subway train	100,000	100
Propeller plane at takeoff	1,000,000	120
Jet engine at takeoff (pain threshold)	10,000,000	140

The range of amplitudes we can encounter in the environment is extremely large, as shown in **Table 11.1**, which indicates the relative amplitudes of environmental sounds, ranging from a whisper to a jet taking off. When we discuss how amplitude is perceived, later in the chapter, we will see that the amplitude of a sound wave is associated with the loudness of a sound.

We can dramatize how large the range of amplitudes is as follows: If the pressure change plotted in the middle record of Figure 11.4, in which the sine wave representing a near-threshold sound like a whisper is about ½-inch high on the page, then in order to plot the graph for a very loud sound, such as music at a rock concert, you would need to represent the sine wave by a curve several miles high! Because this is somewhat impractical, auditory researchers have devised a unit of sound called the decibel (dB), which converts this large range of sound pressures into a more manageable scale.

METHOD | Using Decibels to Shrink Large Ranges of Pressures

The following equation is used for transforming sound pressure level into decibels:

$$dB = 20 \times \text{logarithm}_{10} (p/p_o)$$

The key term in this equation is "logarithm." Logarithms are often used in situations in which there are extremely large ranges. One example of a large range can be seen in a classic animated film by Charles Eames (1977) called *Powers of Ten*. The first scene shows a person lying on a picnic blanket on a beach. The camera then zooms out, as if the person were being filmed from a spaceship taking off. The rate of zoom increases by a factor of 10 every 10 seconds, so the "spaceship's" speed and view increase extremely rapidly. From the 10 × 10 meter scene showing the man on the blanket the scene becomes 100 meters on a side, so Lake Michigan becomes visible, and as the camera speeds away at faster and faster rates, it reaches 10,000,000 meters, so the Earth is

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visible, and eventually 1,000 million million meters near the edge of the Milky Way. The film actually continues to zoom out, until reaching the outer limits of the universe. But we will stop here!

When numbers become this huge, they become difficult to deal with, especially if they need to be plotted on a graph. Logarithms come to the rescue by converting numbers into exponents or powers. The logarithm of a number is the exponent to which the base, which is 10 for *common logarithms*, has to be raised to produce that number. Other bases are used for different applications. For example, logarithms to the base 2, called binary logarithms, are used in computer science.

Common logarithms are illustrated in **Table 11.2**. The logarithm of 10 is 1 because the base, 10, has to be raised to the first power to equal 10. The logarithm of 100 is 2 because 10 has to be raised to the second power to equal 100. The main thing to take away from this table is that multiplying a number by 10 corresponds to an increase of just 1 log unit. A log scale, therefore, converts a huge and unmanageable range of numbers to a smaller range that is easier to deal with. Thus the increase in size from 1 to 1,000 million million that occurs as Charles Eames's spaceship zooms out to the edge of the Milky Way is converted into a more manageable scale of 14 log units. The range of sound pressures encountered in the environment, while not as astronomical as the range in Eames's film, ranges from 1 to 10,000,000, which in powers of 10 is a range of 7 log units.

Let's now return to our equation, dB = 20 × logarithm (p/p_o). According to this equation, decibels are 20 times the logarithm of a ratio of two pressures: p, the pressure of the sound we are considering; and p_o, the reference pressure, usually set at 20 micropascals, which is the pressure near hearing threshold for a 1,000-Hz tone. Let's consider this calculation for two sound pressures.

If the sound pressure, p, is 2,000 micropascals, then

$$dB = 20 \times \log(2{,}000/20) = 20 \times \log 100$$

and since the log of 100 is 2,

$$dB = 20 \times 2 = 40$$

If we multiply the sound pressure by 10 so p is 20,000 micropascals, then

$$dB = 20 \times \log(20{,}000/20) = 20 \times \log 1{,}000$$

The log of 1,000 is 3, so

$$dB = 20 \times 3 = 60$$

Notice that multiplying sound pressure by 10 causes an increase of 20 decibels. Thus, looking back at Table 11.1, we can see that when the sound pressure increases from 1 to 10,000,000, the decibels increase only from 0 to 140. This means that we don't have to deal with graphs that are several miles high!

When specifying the sound pressure in decibels, the notation SPL, for sound pressure level, is added to indicate that decibels were determined using the standard pressure p_o of 20 micropascals. In referring to the sound pressure of a sound stimulus in decibels, the term level or sound level is usually used.

Table 11.2 Common Logarithms

NUMBER	POWER OF 10	LOGARITHM
10	10^1	1
100	10^2	2
1,000	10^3	3
10,000	10^4	4

Complex Tones and Frequency Spectra

We have been using pure tones to illustrate frequency and amplitude. Pure tones are important because they are the fundamental building blocks of sounds, and pure tones have been used extensively in auditory research. Pure tones are, however, rare in the environment. As noted earlier, sounds in the environment, such as those produced by most musical instruments or people speaking, have waveforms that are more complex than the pure tone's sine-wave pattern of pressure changes.

Figure 11.5a shows the pressure changes associated with a complex tone that would be created by a musical instrument.

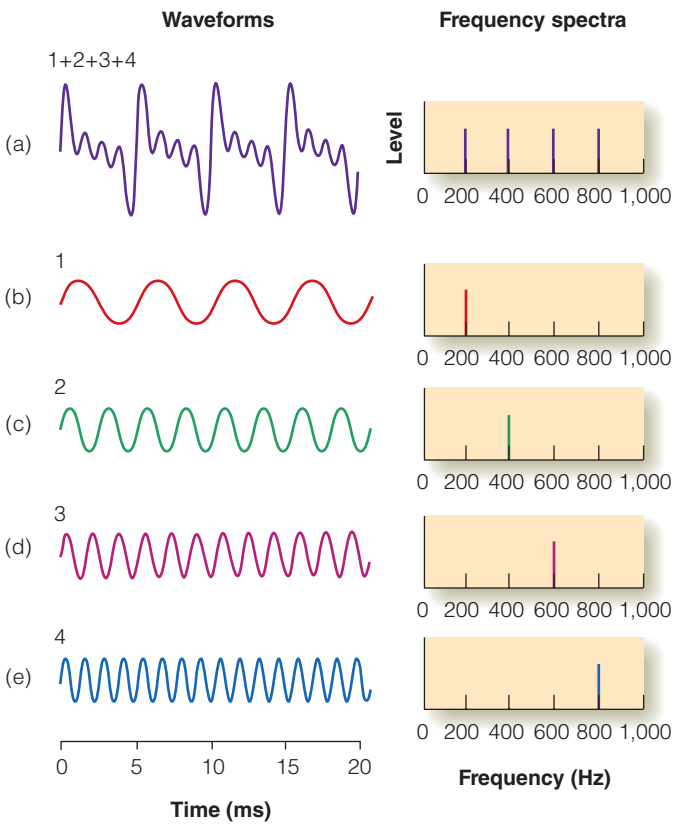

Figure 11.5 Left: Waveforms of tones. Vertical excursions indicate changes in pressure. Horizontal time scale is shown below. (a) A complex periodic sound with a fundamental frequency of 200 Hz. The vertical axis is "pressure." (b) Fundamental (first harmonic) = 200 Hz; (c) second harmonic = 400 Hz; (d) third harmonic = 600 Hz; (e) fourth harmonic = 800 Hz. Right: Frequency spectra for each of the tones on the left. (Adapted from Plack, 2005)

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Notice that the waveform repeats (for example, the waveform in Figure 11.5a repeats four times). This property of repetition means that this complex tone, like a pure tone, is a **periodic waveform**. From the time scale at the bottom of the figure, we see that the tone repeats four times in 20 msec. Because 20 msec is 20/1,000 sec = 1/50 sec, this means that the pattern for this tone repeats 200 times per second. That repetition rate is called the **fundamental frequency** of the tone.

Complex tones like the one in Figure 11.5a are made up of a number of pure tone (sine-wave) components added together. Each of these components is called a **harmonic** of the tone. The **first harmonic**, a pure tone with frequency equal to the fundamental frequency, is usually called the **fundamental** of the tone. The fundamental of this tone, shown in **Figure 11.5b**, has a frequency of 200 Hz, which matches the repetition rate of the complex tone.

Higher harmonics are pure tones with frequencies that are whole-number (2, 3, 4, etc.) multiples of the fundamental frequency. This means that the second harmonic of our complex tone has a frequency of 200 × 2 = 400 Hz (Figure 11.5c), the third harmonic has a frequency of 200 × 3 = 600 Hz (Figure 11.5d), and so on. These additional tones are the higher harmonics of the tone. Adding the fundamental and the higher harmonics in Figures 11.5b, c, d, and e results in the waveform of the complex tone (that is, Figure 11.5a).

Another way to represent the harmonic components of a complex tone is by **frequency spectra**, shown on the right of Figure 11.5. Notice that the horizontal axis is *frequency*, not *time*, as is the case for the waveform plot on the left. The position of each line on the horizontal axis indicates the frequency of one of the tone's harmonics, and the height of the line indicates the harmonic's amplitude. Frequency spectra provide a way of indicating a complex tone's fundamental frequency and harmonics that add up to the tone's complex waveform.

Although a repeating sound wave is composed of harmonics with frequencies that are whole-number multiples of the fundamental frequency, not all the harmonics need to be present for the repetition rate to stay the same. **Figure 11.6** shows what happens if we remove the first harmonic of a complex tone. The tone in **Figure 11.6a** is the one from Figure 11.5a, which has a fundamental frequency of 200 Hz. The tone in **Figure 11.6b** is the same tone with the first harmonic (200 Hz) removed, as indicated by the frequency spectrum on the right. Note that removing a harmonic changes the tone's waveform, but that the rate of repetition remains the same. Even though the fundamental is no longer present, the 200-Hz repetition rate corresponds to the frequency of the fundamental. The same effect also occurs when removing higher harmonics. Thus, if the 400-Hz second harmonic is removed, the tone's waveform changes, but the repetition rate is still 200.

You may wonder why the repetition rate remains the same even though the fundamental or higher harmonics have been removed. Looking at the frequency spectra on the right, we can see that the spacing between harmonics equals the repetition rate. When the fundamental is removed, this spacing remains, so there is still information in the waveform indicating the frequency of the fundamental.

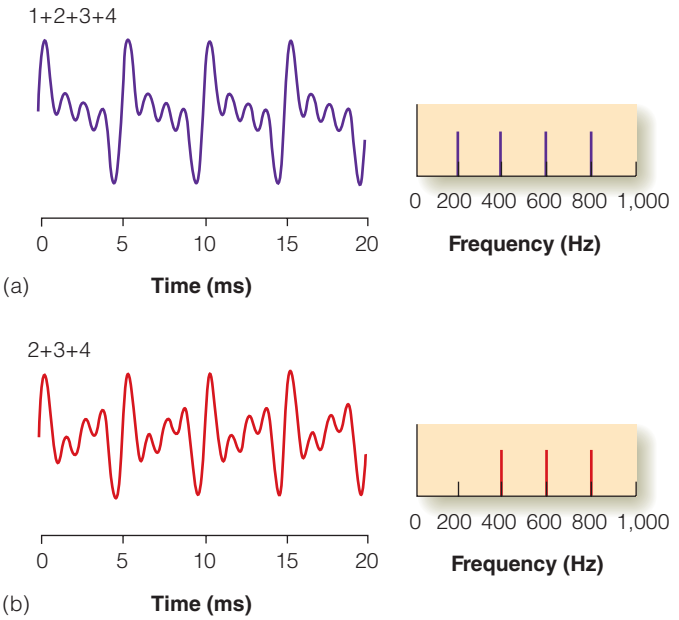

Figure 11.6 (a) The complex tone from Figure 11.5a and its frequency spectrum; (b) the same tone with its first harmonic removed. (Adapted from Plack, 2005)

11.2 Perceptual Aspects of Sound

Our discussion so far has been focused on *physical aspects of the sound stimulus*. Everything we have described so far can be measured by a sound meter that registers pressure changes in the air. A person need not be present, as occurs in our example of a tree falling in the forest when no one is there to hear it. But now let's add a person (or an animal) and consider what people actually *hear*. We will consider two perceptual dimensions: (1) *loudness*, which involves differences in the perceived magnitude of a sound, illustrated by the difference between a whisper and a shout; and (2) *pitch*, which involves differences in the low to high quality of sounds, illustrated by what we hear playing notes from left to right on a piano keyboard.

Thresholds and Loudness

We consider loudness by asking the following two questions about sound: "Can you hear it?" and "How loud does it sound?" These two questions come under the heading of thresholds (the smallest amount of sound energy that can just barely be detected) and loudness (the perceived intensity of a sound that ranges from "just audible" to "very loud").

Loudness and Level Loudness is the perceptual quality most closely related to the *level* or *amplitude* of an auditory stimulus, which is expressed in decibels. Thus, decibels are often associated with loudness, as shown in Table 11.1, which indicates that a sound of 0 dB SPL is just barely detectible and 120 dB SPL is extremely loud (and can cause permanent damage to the receptors inside the ear).

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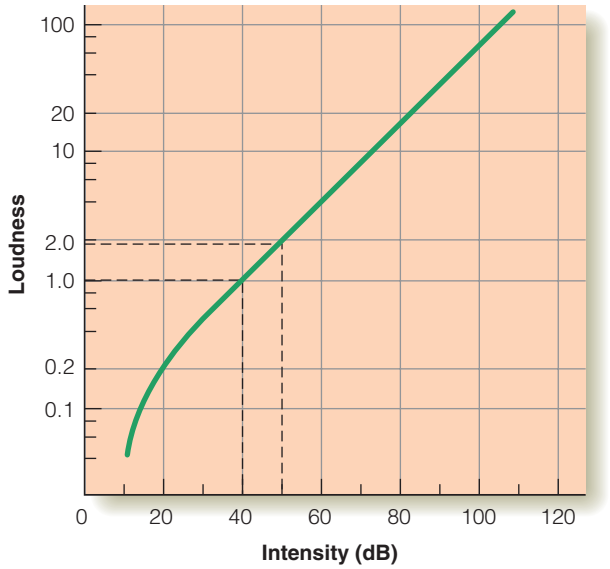

Figure 11.7 Loudness of a 1,000 Hz tone as a function of intensity, determined using magnitude estimation. (Adapted from Gulick et al., 1989)

The relationship between level in decibels (physical) and loudness (perceptual) was determined by S. S. Stevens, using the magnitude estimation procedure (see Chapter 1, page 16; Appendix B, page 418). **Figure 11.7** shows the relationship between decibels and loudness for a 1,000-Hz pure tone. In this experiment, loudness was judged relative to a 40-dB SPL tone, which was assigned a value of 1. Thus, a pure tone that sounds 10 times louder than the 40-dB SPL tone would be judged to have a loudness of 10. The dashed lines indicate that increasing the sound level by 10 dB (from 40 to 50) almost doubles the sound's loudness.

It would be tempting to conclude from Table 11.1 and the curve in Figure 11.7 that "higher decibels" equals greater loudness. But it isn't quite that simple, because thresholds and loudness depend not only on decibels but also on frequency. One way to appreciate the importance of frequency in the perception of loudness is to consider the *audibility curve*.

Thresholds Across the Frequency Range: The Audibility Curve A basic fact about hearing is that we only hear within a specific range of frequencies. This means that there are some frequencies we can't hear, and that even within the range of frequencies we can hear, some are easier to hear than others. Some frequencies have low thresholds—it takes very little sound pressure change to hear them; other frequencies have high thresholds—large changes in sound pressure are needed to make them heard. This is illustrated by the curve in **Figure 11.8**, called the audibility curve. This audibility curve, which indicates the threshold for hearing versus frequency, indicates that we can hear sounds between about 20 Hz and 20,000 Hz and that we are most sensitive (the threshold for hearing is lowest) at frequencies between 2,000 and 4,000 Hz, which happens to be the range of frequencies that is most important for understanding speech.

The light green area above the audibility curve is called the auditory response area because we can hear tones that fall

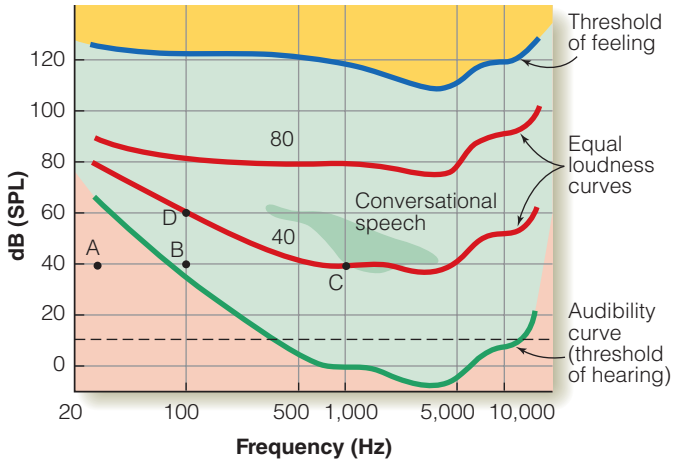

Figure 11.8 The audibility curve and the auditory response area. Hearing occurs in the light green area between the audibility curve (the threshold for hearing) and the upper curve (the threshold for feeling). Tones with combinations of dB and frequency that place them in the light red area below the audibility curve cannot be heard. Tones above the threshold of feeling result in pain. The frequencies between the places where the dashed line at 10 dB crosses the audibility function indicate which frequencies can be heard at 10 dB SPL. (From Fletcher & Munson, 1933)

within this area. At intensities below the audibility curve, we can't hear a tone. For example, we wouldn't be able to hear a 30-Hz tone at 40 dB SPL (point A). The upper boundary of the auditory response area is the curve marked "threshold of feeling." Tones with these high amplitudes are the ones we can "feel"; they can become painful and can cause damage to the auditory system. Although humans hear frequencies between about 20 Hz and 20,000 Hz, other animals can hear frequencies outside the range of human hearing. Elephants can hear stimuli below 20 Hz. Above the high end of the human range, dogs can hear frequencies above 40,000 Hz, cats can hear above 50,000 Hz, and the upper range for dolphins extends as high as 150,000 Hz.

But what happens between the audibility curve and the threshold of feeling? To answer this question, we can pick any frequency and select a point, such as point B, that is just slightly above the audibility curve. Because that point is just above threshold, it will sound very soft. However, as we increase the level by moving up the vertical line, the loudness increases (also see Figure 11.7). Thus, each frequency has a threshold or "baseline"—the decibels at which it can just barely be heard, as indicated by the audibility curve—and loudness increases as we increase the level above this baseline.

Another way to understand the relationship between loudness and frequency is by looking at the red equal loudness curves in Figure 11.8. These curves indicate the sound levels that create the same perception of loudness at different frequencies. An equal loudness curve is determined by presenting a standard pure tone of one frequency and level and having a listener adjust the level of pure tones with frequencies across the range of hearing to match the loudness of the standard. For example, the curve marked 40 in Figure 11.8 was determined by matching the loudness of frequencies across the range of hearing to the loudness of a 1,000-Hz 40-dB SPL tone (point C).

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This means that a 100-Hz tone needs to be played at 60 dB (point D) to have the same loudness as the 1,000-Hz tone at 40 dB.

Notice that the audibility curve and the equal loudness curve marked 40 bend up at high and low frequencies, but the equal loudness curve marked 80 is almost flat between 30 and 5,000 Hz, meaning that tones at a level of 80 dB SPL are roughly equally loud between these frequencies. Thus, at threshold, the level can be very different for different frequencies, but at some level above threshold, different frequencies can have a similar loudness at the same decibel level.

Pitch

Pitch, the perceptual quality we describe as "high" or "low," can be defined as *the property of auditory sensation in terms of which sounds may be ordered on a musical scale extending from low to high* (Bendor & Wang, 2005). The idea that pitch is associated with the musical scale is reflected in another definition of pitch, which states that *pitch is that aspect of auditory sensation whose variation is associated with musical melodies* (Plack, 2014). While often associated with music, pitch is also a property of speech (low-pitched or high-pitched voice) and other natural sounds.

Pitch is most closely related to the physical property of fundamental frequency (the repetition rate of the sound waveform). Low fundamental frequencies are associated with low pitches (like the sound of a tuba), and high fundamental frequencies are associated with high pitches (like the sound of a piccolo). However, remember that pitch is a perceptual, not a physical, property of sound. So pitch can't be measured in a physical way. For example, it isn't correct to say that a sound has a "pitch of 200 Hz." Instead we say that a particular sound has a low pitch or a high pitch, based on how we *perceive* it.

One way to think about pitch is in terms of a piano keyboard. Hitting a key on the left of the keyboard creates a low-pitched rumbling "bass" tone; moving up the keyboard creates higher and higher pitches, until tones on the far right are high-pitched and might be described as "tinkly." The *physical* property that is related to this low to high perceptual experience is *fundamental frequency*, with the lowest note on the piano having a fundamental frequency of 27.5 Hz and the highest note 4,186 Hz (**Figure 11.9**). The perceptual experience of increasing pitch that accompanies increases in a tone's fundamental frequency is called **tone height**.

In addition to the increase in tone height that occurs as we move from the low to the high end of the piano keyboard, something else happens: the letters of the notes A, B, C, D, E, F, and G repeat, and we notice that notes with the same letter sound similar. Because of this similarity, we say that notes with the same letter have the same **tone chroma**. Every time we pass the same letter on the keyboard, we have gone up an interval called an **octave**. Tones separated by octaves have the same tone chroma. For example, each of the As in Figure 11.9, indicated by the arrows, has the same tone chroma.

Notes with the same chroma have fundamental frequencies that are separated by a multiple of two. Thus, A_1 has a fundamental frequency of 27.5 Hz, A_2's is 55 Hz, A_3's is 110 Hz, and so on. This doubling of frequency for each octave results in similar perceptual experiences. Thus, a male with a low-pitched voice and a female with a high-pitched voice can be regarded as singing "in unison," even when their voices are separated by one or more octaves.

While the connection between pitch and fundamental frequency is nicely illustrated by the piano keyboard, there is more to the story than fundamental frequency. If the fundamental or other harmonics of a complex tone are removed, the tone's pitch remains the same, so the two waveforms in Figure 11.6 result in the same pitch. The fact that pitch remains the same, even when the fundamental or other harmonics are removed, is called the **effect of the missing fundamental**. The effect of the missing fundamental has practical consequences. Consider, for example, what happens when you listen to someone talking to you on a land-line phone. Even though the telephone does not reproduce frequencies below about 300 Hz, you can hear the low pitch of a male voice that corresponds to a 100-Hz fundamental frequency because of the pitch created by the higher harmonics (Truax, 1984).

Another way to illustrate the effect of the missing fundamental is to imagine hearing a long tone created by bowing a violin in a quiet room. We then turn on a noisy air conditioner that creates a loud low-frequency hum. Even though the air conditioner noise may make it difficult to hear the lower harmonics of the violin's tone, the tone's pitch remains the same (Oxenham, 2013).

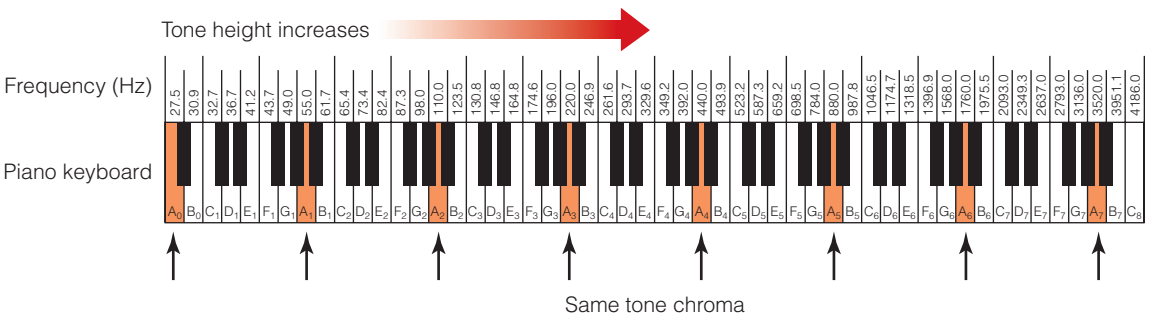

Figure 11.9 A piano keyboard, indicating the frequency associated with each key. Moving up the keyboard to the right increases frequency and tone height. Notes with the same letter, like the As (arrows), have the same tone chroma.

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Timbre

Although removing harmonics does not affect a tone's pitch, another perceptual quality, the tone's **timbre** (pronounced TIM-ber or TAM-ber), does change. Timbre is the quality that distinguishes between two tones that have the same loudness, pitch, and duration, but still sound different. For example, when a flute and an oboe play the same note with the same loudness, we can still tell the difference between these two instruments. We might describe the sound of the flute as *clear* and the sound of the oboe as *reedy*. When two tones have the same loudness, pitch, and duration but sound different, this difference is a difference in timbre.

Timbre is closely related to the harmonic structure of a tone. In **Figure 11.10**, frequency spectra indicate the harmonics of a guitar, a bassoon, and an alto saxophone playing the note G_3 with a fundamental frequency of 196 Hz. Both the relative strengths of the harmonics and the number of harmonics are different in these instruments. For example, the guitar has more high-frequency harmonics than either the bassoon or the alto saxophone. Although the frequencies of the harmonics are always multiples of the fundamental frequency, harmonics may be absent, as is true of some of the high-frequency harmonics of the bassoon and the alto saxophone. It is also easy to notice differences in the timbre of people's voices. When we describe one person's voice as sounding "nasal" and another's as being "mellow," we are referring to the timbres of their voices.

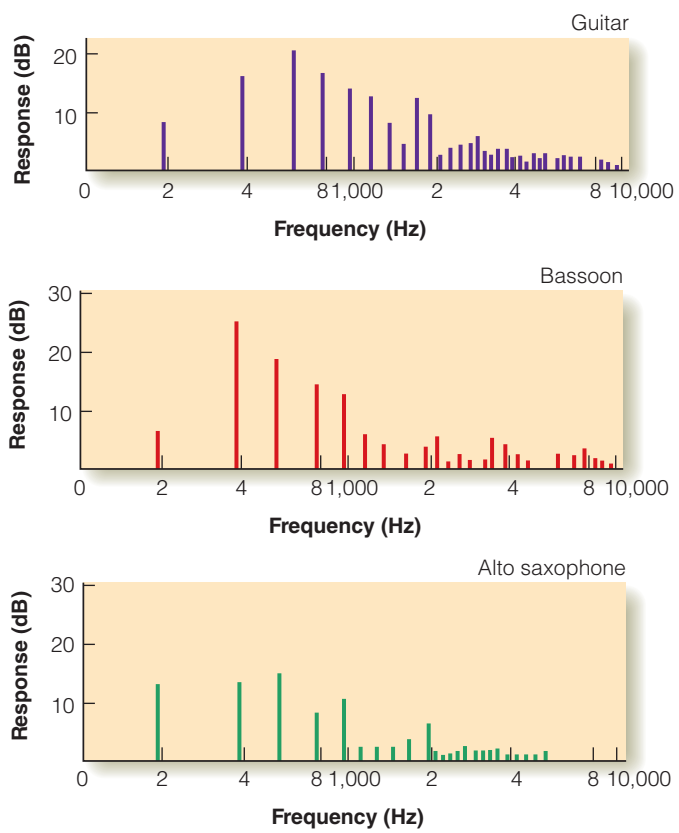

Figure 11.10 Frequency spectra for a guitar, a bassoon, and an alto saxophone playing a tone with a fundamental frequency of 196 Hz. The position of the lines on the horizontal axis indicates the frequencies of the harmonics and their height indicates their intensities. (From Olson, 1967)

The difference in the harmonics of different instruments is not the only factor that creates the distinctive timbres of musical instruments. Timbre also depends on the time course of a tone's **attack** (the buildup of sound at the beginning of the tone) and of the tone's **decay** (the decrease in sound at the end of the tone). Thus, it is easy to tell the difference between a high note played on a clarinet and the same note played on a flute. It is difficult, however, to distinguish between the same instruments when their tones are recorded and the tone's attack and decay are eliminated by erasing the first and last 1/2 second of each tone's recording (Berger, 1964; also see Risset & Mathews, 1969).

Another way to make it difficult to distinguish one instrument from another is to play an instrument's tone backward. Even though this does not affect the tone's harmonic structure, a piano tone played backward sounds more like an organ than a piano because the tone's original decay has become the attack and the attack has become the decay (Berger, 1964; Erickson, 1975). Thus, timbre depends both on the tone's steady-state harmonic structure and on the time course of the attack and decay of the tone's harmonics.

The sounds we have been considering so far—pure tones and the tones produced by musical instruments—are all **periodic sounds**. That is, the pattern of pressure changes in the waveform repeats, as in the tone in Figure 11.5a. There are also aperiodic sounds, which have waveforms that do not repeat. Examples of **aperiodic sounds** would be a door slamming shut, a large group of people talking simultaneously, and noises such as the static on a radio not tuned to a station. Only periodic sounds can generate a perception of pitch. We will focus in this chapter on pure tones and musical tones because these sounds are the ones that have been used in most of the basic research on the operation of the auditory system. In the next section, we will begin considering how the sound stimuli we have been describing are processed by the auditory system so that we can experience sound.

TEST YOURSELF 11.1

1. What are some of the functions of sound? Especially note what information sound provides that is not provided by vision.
2. What are two possible definitions of sound? (Remember the tree falling in the forest.)
3. How is the sound stimulus described in terms of pressure changes in the air? What is a pure tone? Sound frequency?
4. What is the amplitude of a sound? Why was the decibel scale developed to measure amplitude? Is decibel "perceptual" or "physical"?
5. What is a complex tone? What are harmonics? Frequency spectra?

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6. How does removing one or more harmonics from a complex tone affect the repetition rate of the sound stimulus?
7. What is the relationship between sound level and loudness? Which one is physical, and which one is perceptual?
8. What is the audibility curve, and what does it tell us about the relationship between a tone's physical characteristics (level and frequency) and perceptual characteristics (threshold and loudness)?
9. What is pitch? What physical property is it most closely related to? What are tone height and tone chroma?
10. What is the effect of the missing fundamental?
11. What is timbre? Describe the characteristics of complex tones and how these characteristics determine timbre.

11.3 From Pressure Changes to Electrical Signals

Now that we have described the stimuli and their perceptual effects, we are ready to begin describing what happens inside the ear. What we will be describing in this next part of our story is a journey that begins as sound enters the ear and culminates deep inside the ear at the receptors for hearing.

The auditory system accomplishes three basic tasks during this journey. First, it delivers the sound stimulus to the receptors; second, it transduces this stimulus from pressure changes into electrical signals; and third, it processes these electrical signals so they can indicate qualities of the sound source, such as pitch, loudness, timbre, and location.

As we describe this journey, we will follow the sound stimulus through a complex labyrinth on its way to the receptors. But this is not simply a matter of sound moving through one dark tunnel after another. It is a journey in which sound sets structures along the pathway into vibration, with these vibrations being transmitted from one structure to another, starting with the eardrum at the beginning and ending with the vibration of small hairlike parts of the hearing receptors called *stereocilia* deep within the ear. The ear is divided into three divisions: outer, middle, and inner. We begin with the outer ear.

The Outer Ear

Sound waves first pass through the **outer ear**, which consists of the **pinnae**, the structures that stick out from the sides of the head, and the **auditory canal**, a tubelike recess about 3 cm long in adults (**Figure 11.11**). Although the pinnae are the most obvious part of the ear and help us determine the location of sounds, as we will see in Chapter 12, it is the part of the ear we could most easily do without. Van Gogh did *not* make himself deaf in his left ear when he attacked his pinna with a razor in 1888.

The auditory canal protects the delicate structures of the middle ear from the hazards of the outside world. The auditory canal's 3-cm recess, along with its wax, protects the delicate

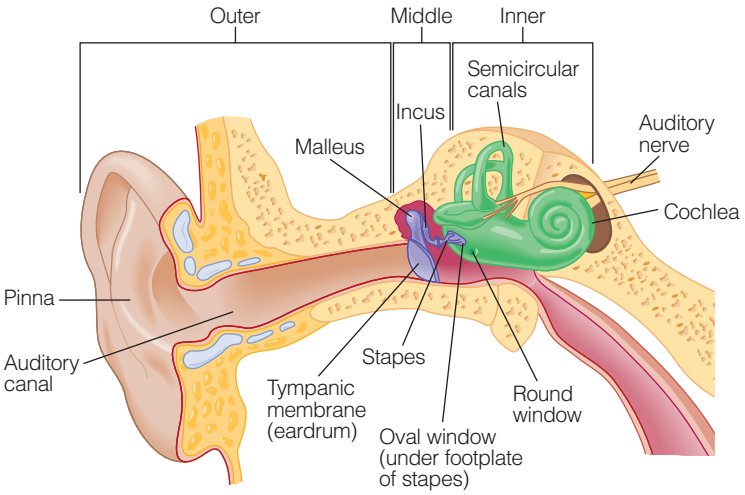

Figure 11.11 The ear, showing its three subdivisions—outer, middle, and inner. (From Lindsay & Norman, 1977)

tympanic membrane, or **eardrum**, at the end of the canal and helps keep this membrane and the structures in the middle ear at a relatively constant temperature.

In addition to its protective function, the auditory canal has another effect: to enhance the intensities of some sounds by means of the physical principle of resonance. **Resonance** occurs in the auditory canal when sound waves that are reflected back from the closed end of the auditory canal interact with sound waves that are entering the canal. This interaction reinforces some of the sound's frequencies, with the frequency that is reinforced the most being determined by the length of the canal. The frequency reinforced the most is called the **resonant frequency** of the canal.

Measurements of the sound pressures inside the ear indicate that the resonance that occurs in the auditory canal has a slight amplifying effect that increases the sound pressure level of frequencies between about 1,000 and 5,000 Hz, which, as we can see from the audibility curve in Figure 11.8, covers the most sensitive range of human hearing.

The Middle Ear

When airborne sound waves reach the tympanic membrane at the end of the auditory canal, they set it into vibration, and this vibration is transmitted to structures in the middle ear, on the other side of the tympanic membrane. The **middle ear** is a small cavity, about 2 cubic centimeters in volume, that separates the outer and inner ears (**Figure 11.12**). This cavity contains the **ossicles**, the three smallest bones in the body. The first of these bones, the **malleus** (also known as the *hammer*), is set into vibration by the tympanic membrane, to which it is attached, and transmits its vibrations to the **incus** (or *anvil*), which, in turn, transmits its vibrations to the **stapes** (or *stirrup*). The stapes then transmits its vibrations to the inner ear by pushing on the membrane covering the **oval window**.

Why are the ossicles necessary? We can answer this question by noting that both the outer ear and middle ear are filled with air, but the inner ear contains a watery liquid that is much

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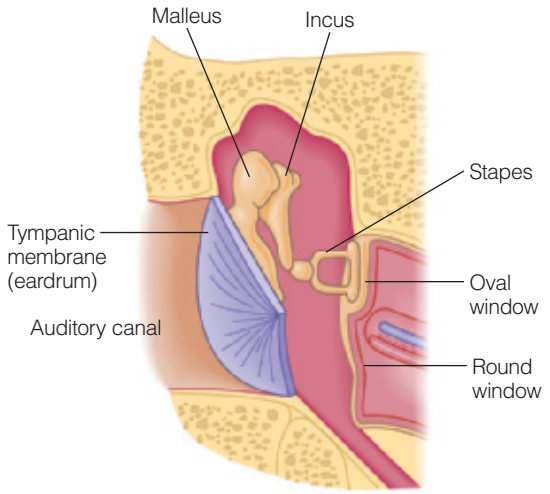

Figure 11.12 The middle ear. The three bones of the middle ear transmit the vibrations of the tympanic membrane to the inner ear.

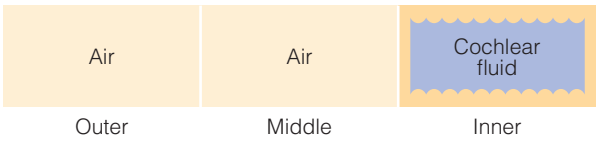

Figure 11.13 Environments inside the outer, middle, and inner ears. The fact that liquid fills the inner ear poses a problem for the transmission of sound vibrations from the air of the middle ear.

denser than the air (**Figure 11.13**). The mismatch between the low density of the air and the high density of this liquid creates a problem: pressure changes in the air are transmitted poorly to the much denser liquid. This mismatch is illustrated by the difficulty you would have hearing people talking to you if you were underwater and they were above the surface.

If vibrations had to pass directly from the air in the middle ear to the liquid in the inner ear, less than 1 percent of the vibrations would be transmitted (Durrant & Lovrinic, 1977). The ossicles help solve this problem in two ways: (1) by concentrating the vibration of the large tympanic membrane onto the much smaller stapes, which increases the pressure by a factor of about 20 (**Figure 11.14a**); and (2) by being hinged to create a lever action—an effect similar to what happens when a fulcrum is placed under a board, so that pushing down on the long end of the board makes it possible to lift a heavy weight on the short end (**Figure 11.14b**). We can appreciate the effect of the ossicles by noting that in patients whose ossicles have been damaged beyond surgical repair, it is necessary to increase the sound pressure by a factor of 10 to 50 to achieve the same hearing as when the ossicles were functioning (Bess & Humes, 2008).

Not all animals require the concentration of pressure and lever effect provided by the ossicles in the human ear. For example, there is only a small mismatch between the density of water, which transmits sound in a fish's environment, and the liquid inside the fish's ear. Thus, fish have no outer or middle ear.

The middle ear also contains the **middle-ear muscles**, the smallest skeletal muscles in the body. These muscles are

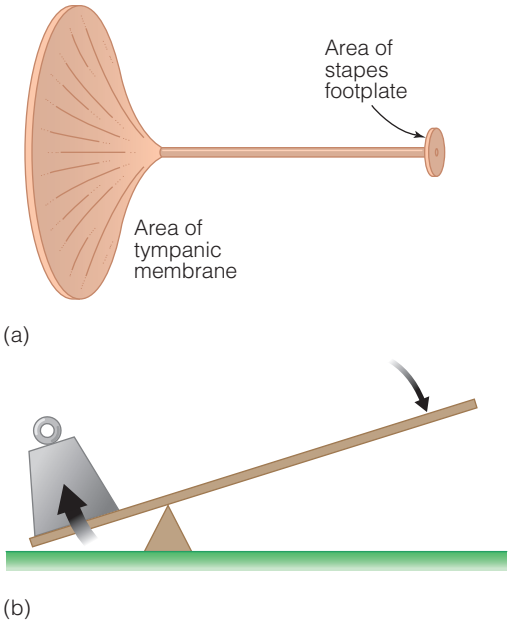

Figure 11.14 (a) A diagrammatic representation of the tympanic membrane and the stapes, showing the difference in size between the two. (b) How lever action can amplify a small force, presented on the right, to lift the large weight on the left. The lever action of the ossicles amplifies the sound vibrations reaching the tympanic inner ear. (From Schubert, 1980)

attached to the ossicles, and at very high sound levels they contract to dampen the ossicles' vibration. This reduces the transmission of low-frequency sounds and helps to prevent intense low-frequency components from interfering with our perception of high frequencies. In particular, contraction of the muscles may prevent our own vocalizations, and sounds from chewing, from interfering with our perception of speech from other people—an important function in a noisy restaurant!

The Inner Ear

We will describe first the structure of the inner ear, and then what happens when structures of the inner ear are set into vibration.

Inner Ear Structure The main structure of the **inner ear** is the liquid-filled **cochlea**, the snaillike structure shown in green in Figure 11.11, and shown partially uncoiled in **Figure 11.15a**. **Figure 11.15b** shows the cochlea completely uncoiled to form a long straight tube. The most obvious feature of the uncoiled cochlea is that the upper half, called the *scala vestibuli*, and the lower half, called the *scala tympani*, are separated by a structure called the **cochlear partition**. This partition extends almost the entire length of the cochlea, from its base near the stapes to its apex at the far end. Note that this diagram is not drawn to scale and so does not show the cochlea's true proportions. In reality, the uncoiled cochlea would be a cylinder 2 mm in diameter and 35 mm long.

Although the cochlear partition is indicated by a thin line in Figure 11.15b, it is actually relatively large and contains the

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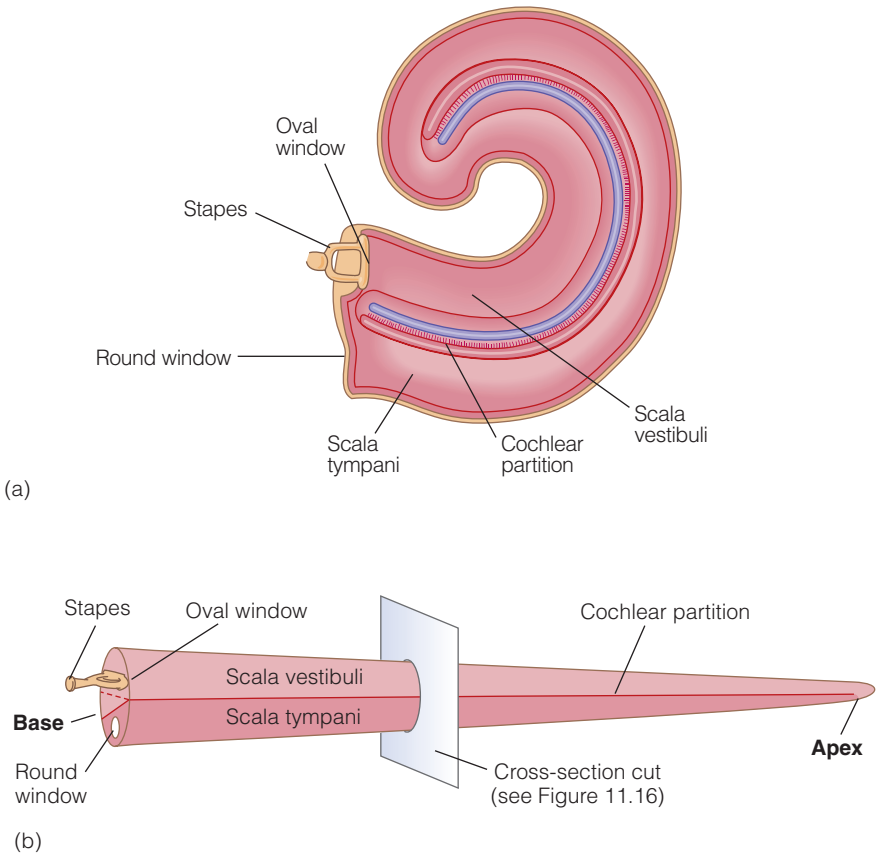

Figure 11.15 (a) A partially uncoiled cochlea. (b) A fully uncoiled cochlea. The cochlear partition, which is indicated here by a line, actually contains the basilar membrane and the organ of Corti, as shown in Figure 11.16.

structures that transform the vibrations inside the cochlea into electricity. We can see the structures within the cochlear partition by taking a cross-section cut of the cochlea, as shown in Figure 11.15b, and looking at the cochlea end-on and in cross section, as in **Figure 11.16a**. When we look at the cochlea in this way, we see the **organ of Corti**, which contains the **hair cells**, the receptors for hearing. It is important to remember that Figure 11.16 shows just one place along the organ of Corti, but as shown in Figure 11.15, the cochlear partition, which contains the organ of Corti, extends the entire length of the cochlea. There are, therefore, hair cells from one end of the cochlea to the other. In addition, there are two membranes, the **basilar membrane** and the **tectorial membrane**, which also extend the length of the cochlea, and which play crucial roles in activating the hair cells.

The hair cells are shown in red in **Figure 11.16b** and in yellow in **Figure 11.17**. At the tips of the hair cells are small processes called **stereocilia**, which bend in response to pressure changes. The human ear contains one row of **inner hair cells** and about three rows of **outer hair cells**, with about 3,500 inner hair cells and 12,000 outer hair cells. The stereocilia of the tallest row of outer hair cells are embedded in the tectorial

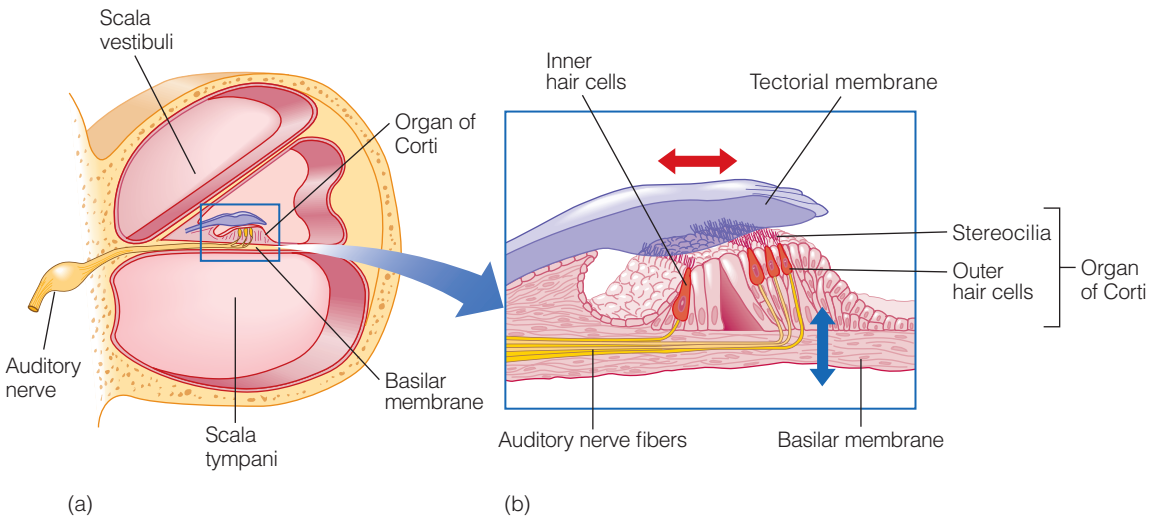

Figure 11.16 (a) Cross section of the cochlea. (b) Close-up of the organ of Corti, showing how it rests on the basilar membrane. Arrows indicate the motions of the basilar membrane and tectorial membrane that are caused by vibration of the cochlear partition. Although not obvious in this figure, the cilia of the outer hair cells are embedded in the tectorial membrane, but the cilia of the inner hair cells are not.
(Adapted from Denes & Pinson, 1993)

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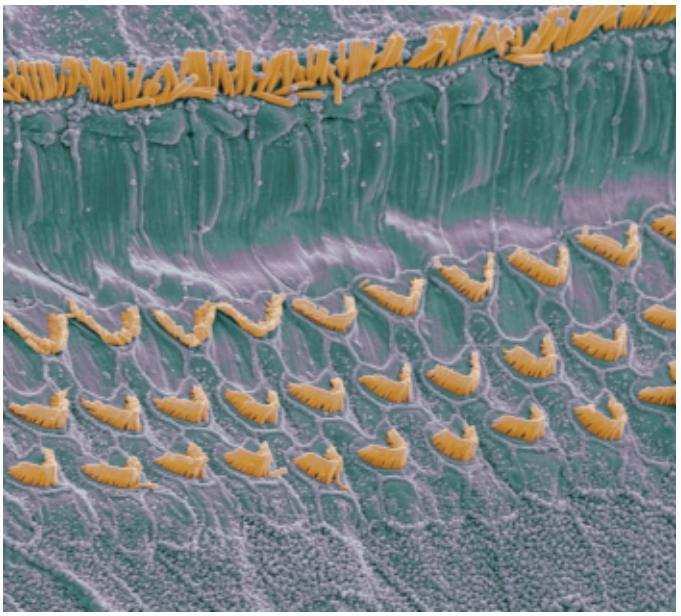

Steve Gschmeissner/Science Photo Library/Corbis

Figure 11.17 Scanning electron micrograph showing inner hair cells (top) and the three rows of outer hair cells (bottom). The hair cells have been colored to stand out.

membrane, and the stereocilia of the rest of the outer hair cells and all of the inner hair cells are not (Moller, 2006).

Vibration Bends the Stereocilia The scene we have described—the organ of Corti sitting on the basilar membrane, with the tectorial membrane arching over the hair cells—is the staging ground for events that occur when vibration of the stapes in the middle ear sets the oval window into motion. The back and forth motion of the oval window transmits vibrations to the liquid inside the cochlea, which sets the basilar membrane into motion (blue arrow in Figure 11.16b). The up-and-down motion of the basilar membrane has two results: (1) it sets the organ of Corti into an up-and-down vibration, and (2) it causes the tectorial membrane to move back and forth, as shown by the red arrow. These two motions mean that the tectorial membrane slides back and forward just above the hair cells. The movement of the tectorial membrane causes the stereocilia of the outer hair cells that are embedded in the membrane to bend. The stereocilia of the other outer hair cells and the inner hair cells also bend, but in response to pressure waves in the liquid surrounding the stereocilia (Dallos, 1996).

Bending Causes Electrical Signals We have now reached the point in our story where the vibrations that have reached the inner ear become transformed into electrical signals. This is the process of transduction we described for vision in Chapter 2, which occurs when the light-sensitive part of a visual pigment molecule absorbs light, changes shape, and triggers a sequence of chemical reactions that ends up affecting the flow of ions (charged molecules) across the visual receptor membrane. As we describe this process for hearing, we will focus on the inner hair cells, because these are the main receptors responsible for generating signals that are sent to the cortex in auditory nerve fibers. We will return to the outer hair cells later in the chapter.

Transduction for hearing also involves a sequence of events that creates ion flow. First, the stereocilia of the hair cells bend in one direction (**Figure 11.18a**). This bending causes structures called tip links to stretch, and this opens tiny ion channels in the membrane of the stereocilia, which function like trapdoors. When the ion channels are open, positively charged potassium ions flow into the cell and an electrical signal results. When the stereocilia bend in the other direction (**Figure 11.18b**), the tip links slacken, the ion channels close, and ion flow stops. Thus, the back-and-forth bending of the hair cells causes alternating bursts of electrical signals (when the stereocilia bend in one direction) and no electrical signals (when the stereocilia bend in the opposite direction). The electrical signals in the hair cells result in the release of neurotransmitters at the synapse separating the inner hair cells from the auditory nerve fibers, which causes these auditory nerve fibers to fire.

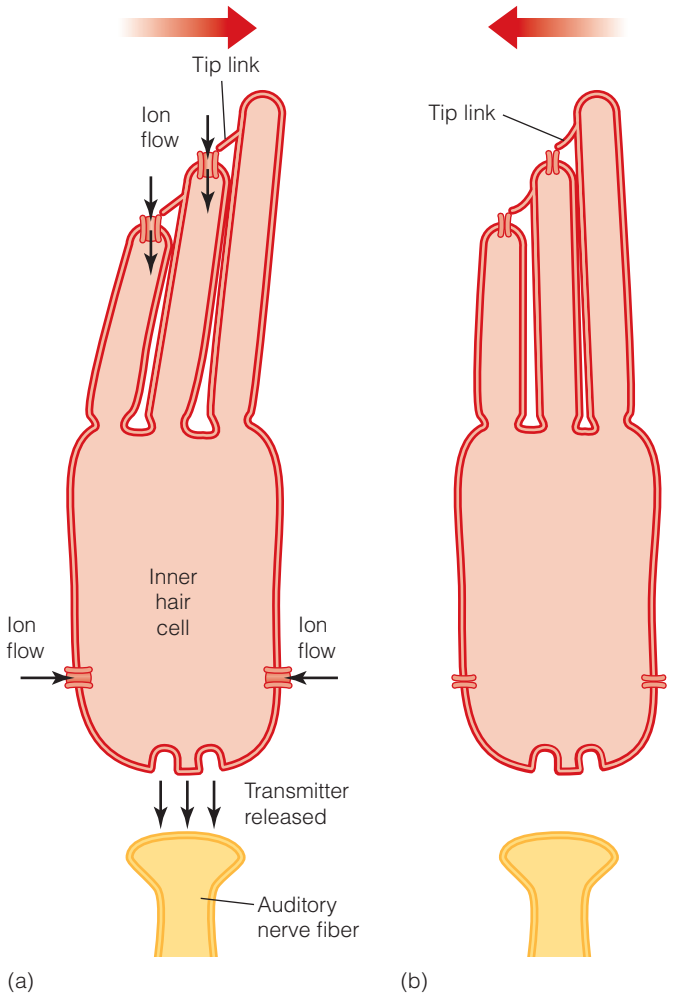

Figure 11.18 How movement of stereocilia causes an electrical change in the hair cell. (a) When the stereocilia are bent to the right, the tip links are stretched and ion channels are opened. Positively charged potassium ions (K+) enter the cell, causing the interior of the cell to become more positive. (b) When the stereocilia move to the left, the tip links slacken, and the channels close. (Based on Plack, 2005)

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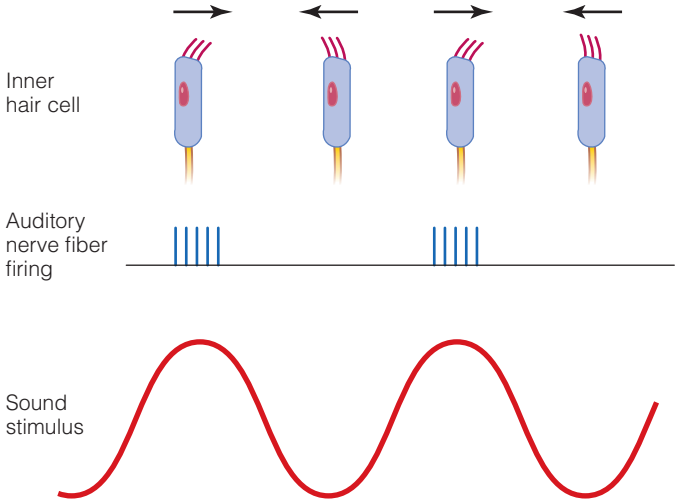

Figure 11.19 How hair cell activation and auditory nerve fiber firing are synchronized with pressure changes of the stimulus. The auditory nerve fiber fires when the cilia are bent to the right. This occurs at the peak of the sine-wave change in pressure.

The Electrical Signals Are Synchronized With the Pressure Changes of a Pure Tone

Figure 11.19 shows how the bending of the stereocilia follows the increases and decreases of the pressure of a pure tone sound stimulus. When the pressure increases, the stereocilia bend to the right, the hair cell is activated, and attached auditory nerve fibers will tend to fire. When the pressure decreases, the stereocilia bend to the left, and no firing occurs. This means that auditory nerve fibers fire in synchrony with the rising and falling pressure of the pure tone.

This property of firing at the same place in the sound stimulus is called phase locking. For high-frequency tones, a nerve fiber may not fire every time the pressure changes because it needs to rest after it fires (see *refractory period*, Chapter 2, page 24). But when the fiber does fire, it fires at the same time in the sound stimulus, as shown in **Figures 11.20a** and **11.20b**. Since many fibers respond to the tone, it is likely that if some "miss" a particular pressure change, other fibers will be firing at that time. Therefore, when we combine the response of many fibers, each of which fires at the peak of the sound wave, the overall firing matches the frequency of the sound stimulus, as shown in **Figure 11.20c**. What this means is that a sound's repetition rate produces a pattern of nerve firing in which the timing of nerve spikes matches the timing of the repeating sound stimulus.

11.4 How Frequency Is Represented in the Auditory Nerve

Now that we know how electrical signals are created, the next question is, how do these signals provide information about a tone's frequency? The search for the answer to the question of how frequency is signaled by activity in the auditory nerve has

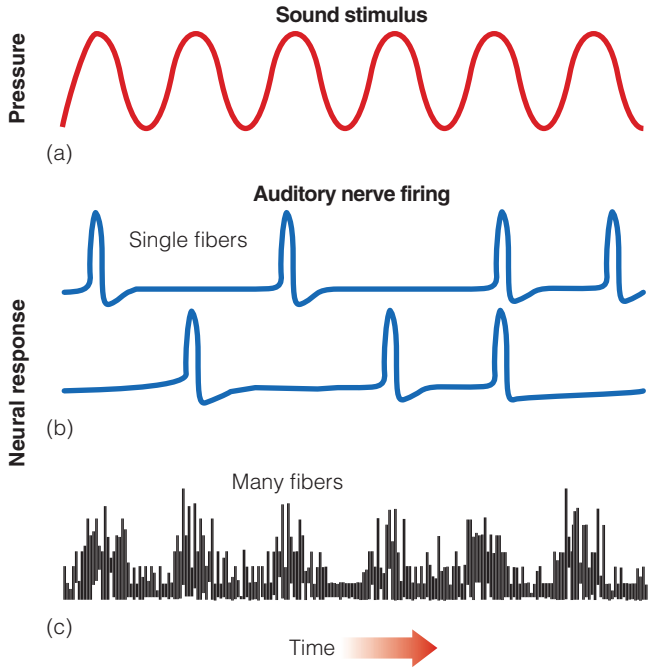

Figure 11.20 (a) Pressure changes for a 250-Hz tone. (b) Pattern of nerve spikes produced by two separate nerve fibers. Notice that the spikes always occur at the peak of the pressure wave. (c) The combined spikes produced by 500 nerve fibers. Although there is some variability in the single neuron response, the response of the large group of neurons represents the periodicity of the 250-Hz tone. (Based on Plack, 2005)

focused on determining how the basilar membrane vibrates to different frequencies. Pioneering research on this problem was carried out by Georg von Békésy (1899–1972), who won the Nobel Prize in physiology and medicine in 1961 for his research on the physiology of hearing.

Békésy Discovers How the Basilar Membrane Vibrates

Békésy determined how the basilar membrane vibrates to different frequencies by observing the vibration of the basilar membrane. He accomplished this by boring a hole in cochleas taken from animal and human cadavers. He presented different frequencies of sound and observed the membrane's vibration by using a technique similar to that used to create stop-action photographs of high-speed events (Békésy, 1960). When he observed the membrane's position at different points in time, he saw the basilar membrane's vibration as a traveling wave, like the motion that occurs when a person holds the end of a rope and "snaps" it, sending a wave traveling down the rope.

Figure 11.21a shows a perspective view of this traveling wave. **Figure 11.21b** shows side views of the traveling wave caused by a pure tone at three successive moments in time. The solid horizontal line represents the basilar membrane at rest. Curve 1 shows the position of the basilar membrane at one moment during its vibration, and curves 2 and 3 show the positions of the membrane at two later moments. Békésy's

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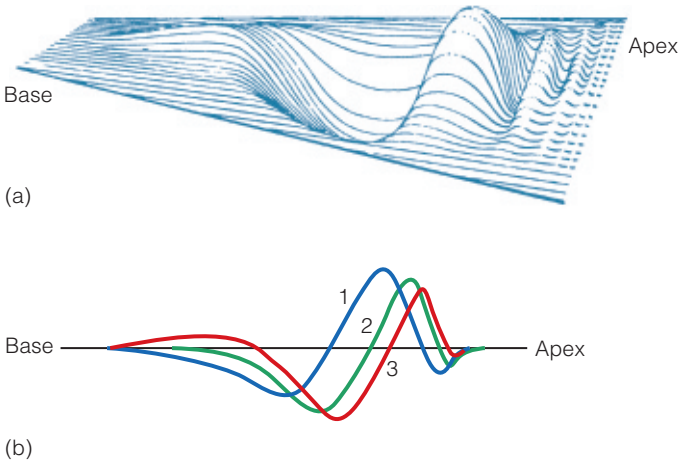

Figure 11.21 (a) A traveling wave like the one observed by Békésy. This picture shows what the membrane looks like when the vibration is "frozen" with the wave about two-thirds of the way down the membrane. (b) Side views of the traveling wave caused by a pure tone, showing the position of the membrane at three instants in time as the wave moves from the base to the apex of the cochlear partition. [(a) Adapted from Tonndorf, 1960; (b) Adapted from Békésy, 1960]

measurements showed that most of the membrane vibrates, but that some parts vibrate more than others.

Although the motion takes the form of a traveling wave, the important thing is what happens at particular points along the basilar membrane. If you were at one point on the basilar membrane you would see the membrane vibrating up and down at the frequency of the tone. If you observed the entire membrane, you would see that vibration occurs over a large portion of the membrane, and that there is one place that vibrates the most.

Békésy's most important finding was that the place that vibrates the most depends on the frequency of the tone, as shown in **Figure 11.22**. The arrows indicate the extent of the up-and-down displacement of the basilar membrane at different places on the membrane. The red arrows indicate the place where the membrane vibrates the most for each frequency. Notice that as the frequency increases, the place on the membrane that vibrates the most moves from the **apex** at the end of the cochlea toward the **base** at the oval window. Thus, the place of maximum vibration, which is near the apex of the basilar membrane for a 25-Hz tone, has moved to nearer the base for a 1,600-Hz tone. Because the place of maximum vibration depends on frequency, this means that basilar membrane vibration effectively functions as a filter that sorts tones by frequency.

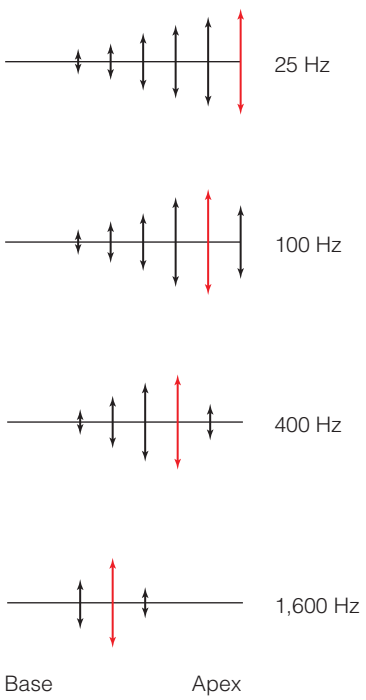

Figure 11.22 The amount of vibration at different locations along the basilar membrane is indicated by the size of the arrows at each location, with the place of maximum vibration indicated in red. When the frequency is 25 Hz, maximum vibration occurs at the apex of the cochlear partition. As the frequency is increased, the location of the maximum vibration moves toward the base of the cochlear partition. (Based on data in Békésy, 1960)

The Cochlea Functions as a Filter

We can appreciate how the cochlea acts like a filter that sorts sound stimuli by frequency by leaving hearing for a moment and considering **Figure 11.23a**, which shows how coffee beans are filtered to sort them by size. Beans with a variety of sizes are

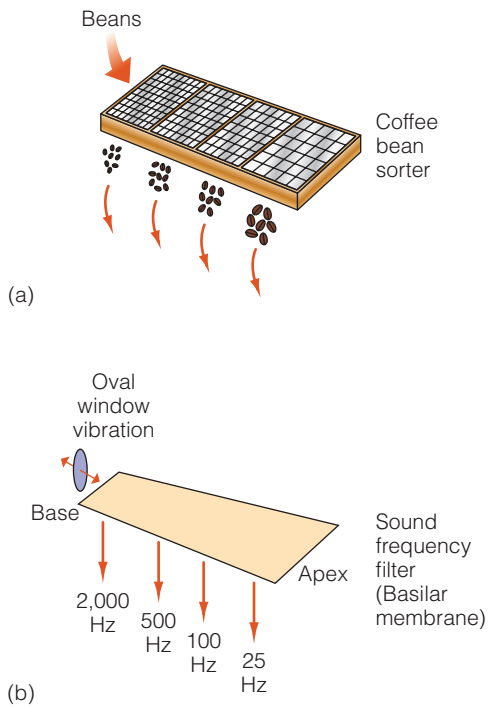

Figure 11.23 Two ways of sorting. (a) Coffee beans of different sizes are deposited at the left end of the sieve. By shaking and gravity, the beans travel down the sieve. Smaller coffee beans drop through the small holes at the beginning of the sieve; larger ones drop through the larger holes near the end. (b) Sound vibrations of different frequencies, which occur at the oval window, on the left, set the basilar vibration into motion. Higher frequencies cause vibration at the base of the basilar membrane, near the oval window. Low frequencies cause vibrations nearer the apex of the basilar membrane.

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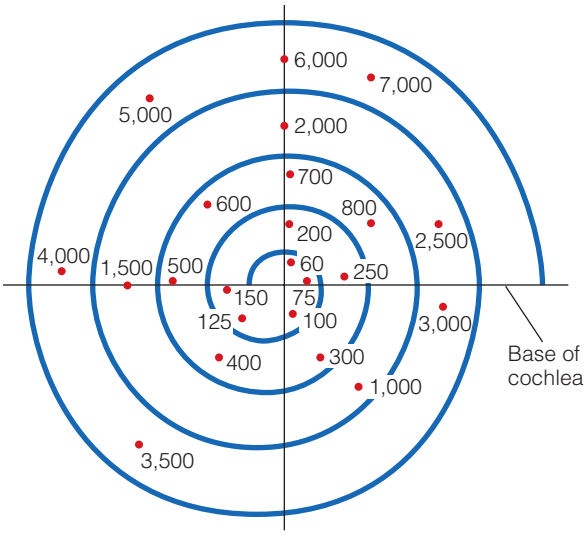

Figure 11.24 Tonotopic map of the guinea pig cochlea. Numbers indicate the location of the maximum electrical response for each frequency. (From Culler et al., 1943)

deposited at one end of a sieve that contains small holes at the beginning and larger holes toward the far end. The beans travel down the sieve, with smaller beans dropping through the first holes and larger and larger beans dropping through holes farther down the sieve. The sieve, therefore, filters coffee beans by size.

Just as the different sized holes along the length of the sieve separate coffee beans by size, the different places of maximum vibration along the length of the basilar membrane separate sound stimuli by frequency (**Figure 11.23b**). High frequencies cause more vibration near the base end of the cochlea, and low frequencies cause more vibration at the apex of the cochlea. Thus, vibration of the basilar membrane "sorts" or "filters" by frequency so hair cells are activated at different places along the cochlea for different frequencies.

Figure 11.24 shows the results of measurements made by placing electrodes at different positions on the outer surface of a guinea pig's cochlea and stimulating with different frequencies (Culler, 1935; Culler et al., 1943). This "map" of the cochlear illustrates the sorting of frequencies, with high frequencies activating the base of the cochlea and low frequencies activating the apex. This map of frequencies is called a tonotopic map.

Another way of demonstrating the connection between frequency and place is to record from single auditory nerve fibers located at different places along the cochlea. Measurement of the response of auditory nerve fibers to frequency is depicted by a fiber's *neural frequency tuning curve*.

METHOD | Neural Frequency Tuning Curves

A neuron's frequency tuning curve is determined by presenting pure tones of different frequencies and measuring the sound level necessary to cause the neuron to increase its firing above the baseline or "spontaneous" rate in the absence of sounds.

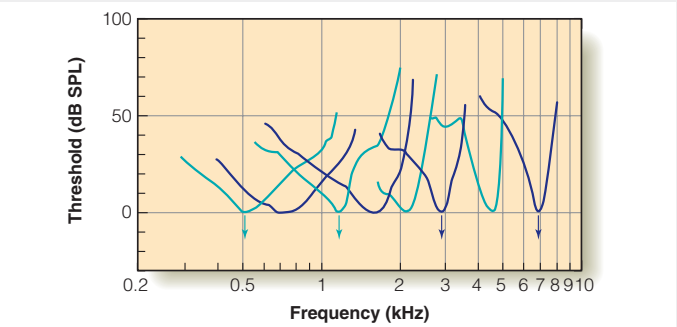

Figure 11.25 Frequency tuning curves of cat auditory nerve fibers. The characteristic frequencies of some of the fibers are indicated by the arrows pointing to the frequency axis. The frequency scale is in kilohertz (kHz), where 1 kHz = 1,000 Hz. Only a small number of curves are shown here. Each of the 3,500 inner hair cells has its own tuning curve, and because each inner hair cell sends signals to about 20 auditory nerve fibers, each frequency is represented by a number of neurons located at that frequency's place along the basilar membrane. (Adapted from Miller et al., 1997)

This level is the threshold for that frequency. Plotting the threshold for each frequency results in frequency tuning curves like the ones in **Figure 11.25**. The arrows under some of the curves indicates the frequency to which the neuron is most sensitive (has the lowest sound level threshold). This frequency is called the characteristic frequency of the particular auditory nerve fiber.

The cochlea's filtering action is reflected by the fact that (1) the neurons respond best to one frequency and (2) each frequency is associated with nerve fibers located at a specific place along the basilar membrane, with fibers originating near the base of the cochlea having high characteristic frequencies and those originating near the apex having low characteristic frequencies.

The Outer Hair Cells Function as Cochlear Amplifiers

While Békésy's measurements located the places where specific frequencies caused maximum vibration along the basilar membrane, he also observed that this vibration was spread out over a large portion of the membrane. Later researchers realized that one reason for Békésy's broad vibration patterns was that his measurements were carried out on "dead" cochleas that were isolated from animal and human cadavers. When modern researchers used more advanced technology that enabled them to measure vibration in live cochleas, they showed that the pattern of vibration for specific frequencies was much narrower than what Békésy had observed (Khanna & Leonard, 1982; Rhode, 1971, 1974). But what was responsible for this narrower vibration? In 1983 Hallowell Davis published a paper titled "An Active Process in Cochlear Mechanics," which began with the attention-getting statement: "We are in the midst of a major breakthrough in auditory

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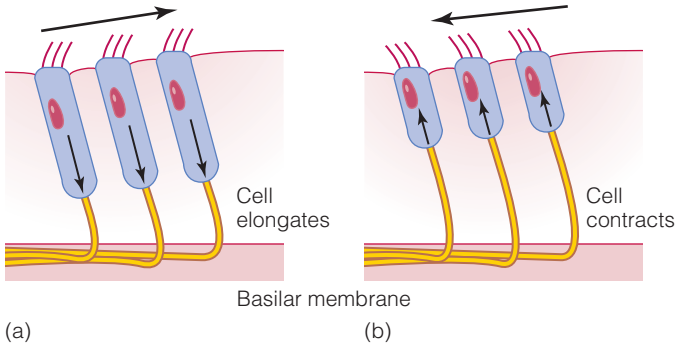

Figure 11.26 The outer hair cell cochlear amplifier mechanism occurs when the cells (a) elongate when stereocilia bend in one direction and (b) contract when the stereocilia bend in the other direction. This results in an amplifying effect on the motion of the basilar membrane.

physiology." He went on to propose a mechanism that he named the **cochlear amplifier**, which explained why neural turning curves were narrower than what would be expected based on Békésy's measurements of basilar membrane vibration.

Davis proposed that the cochlear amplifier was an active mechanical process that took place in the outer hair cells. We can appreciate what this active mechanical process is by describing how the outer hair cells respond to and influence the vibration of the basilar membrane.[1]

The major purpose of outer hair cells is to influence the way the basilar membrane vibrates, and they accomplish this by changing length (Ashmore, 2008; Ashmore et al., 2010). While ion flow in inner hair cells causes an electrical response in auditory nerve fibers, ion flow in outer hair cells causes mechanical changes inside the cell that causes the cell to expand and contract, as shown in **Figure 11.26**. The outer hair cells become elongated when the stereocilia bend in one direction and contract when they bend in the other direction. This mechanical response of elongation and contraction pushes and pulls on the basilar membrane, which increases the motion of the basilar membrane and sharpens its response to specific frequencies.

The importance of the cochlear amplifier is illustrated by the frequency tuning curves in Figure 11.27. The solid blue curve shows the frequency tuning of a cat's auditory nerve fiber with a characteristic frequency of about 8,000 Hz. The dashed red curve shows what happened when the cochlear amplifier was eliminated by destroying the outer hair cells with a chemical that attacked the outer hair cells but left the inner hair cells intact. Whereas originally the fiber had a low threshold at 8,000 Hz, indicated by the arrow, it now takes much higher intensities to get the auditory nerve fiber to respond to 8,000 Hz and nearby frequencies (Fettiplace & Hackney, 2006; Liberman & Dodds, 1984).

The conclusion from **Figure 11.27** and the results of other experiments is that the cochlear amplifier greatly sharpens the tuning of each place along the cochlea.

[1] Theodore Gold (1948), who was to become a well-known researcher in cosmology and astronomy, made the original proposal that there is an active process in the cochlea. But it wasn't until many years later that further developments in auditory research led to the proposal of the cochlear amplifier mechanism (see Gold, 1989).

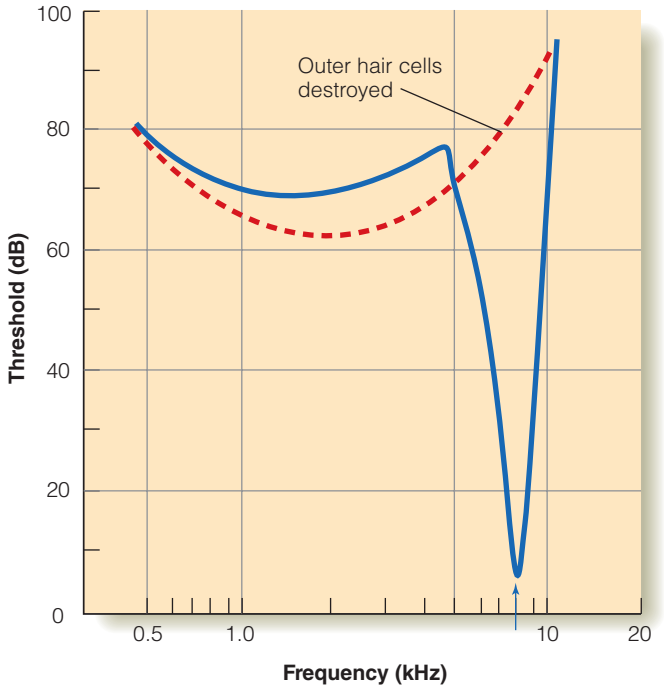

Figure 11.27 Effect of outer hair cell damage on the frequency tuning curve. The solid curve is the frequency tuning curve of a neuron with a characteristic frequency of about 8,000 Hz (arrow). The dashed curve is the frequency tuning curve for the same neuron after the outer hair cells were destroyed by injection of a chemical. (Adapted from Fettiplace & Hackney, 2006)

All of our descriptions so far have been focused on physical events that occur within the inner ear. Our story has featured physical processes such as trapdoors opening and ions flowing, nerve firing that is synchronized with the sound stimulus, and basilar membrane vibrations that separate different frequencies along the length of the cochlea. All of this information is crucial for understanding how the ear functions. The next section will look at the connection between these physical processes and perception.

TEST YOURSELF 11.2

1. Describe the structure of the ear, focusing on the role that each component plays in transmitting the vibrations that enter the outer ear to the auditory receptors in the inner ear.
2. Focusing on the inner ear, describe (a) what causes the bending of the stereocilia of the hair cells; (b) what happens when the stereocilia bend; (c) how phase locking causes the electrical signal to follow the timing of the sound stimulus.
3. Describe Békésy's discovery of how the basilar membrane vibrates. Specifically, what is the relationship between sound frequency and basilar membrane vibration?
4. What does it mean to say that the cochlea acts as a filter? How is this supported by the tonotopic map and by neural frequency tuning curves? What is a neuron's characteristic frequency?
5. How do the outer hair cells function as cochlear amplifiers?

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11.5 The Physiology of Pitch Perception: The Cochlea

We are now ready to describe what we know about the relation between physiological events in the auditory system and the perception of pitch. We begin by describing physiological processes in the ear and will then move on to the brain.

Place and Pitch

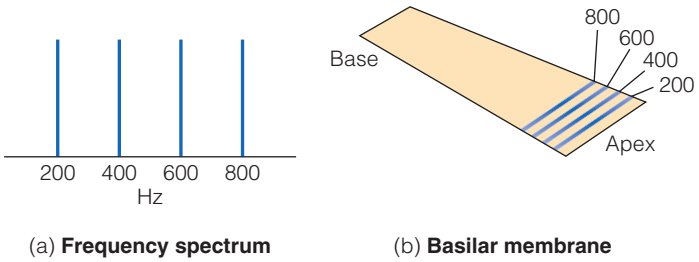
Our starting point is the connection between a tone's frequency and the perception of pitch. Given that low frequencies are associated with low pitch and higher frequencies with higher pitch, it has been proposed that pitch perception is determined by the firing of neurons that respond best to specific frequencies. This idea follows from Békésy's discovery that specific frequencies cause maximum vibration at specific *places* along the basilar membrane, which creates a tonotopic map like the one in Figure 11.24.

The association of frequency with place led to the following explanation of the physiology of pitch perception: A pure tone causes a peak of activity at a specific place on the basilar membrane. The neurons connected to that place respond strongly to that frequency, as indicated by the auditory nerve fiber frequency tuning curves in Figure 11.25, and this information is carried up the auditory nerve to the brain. The brain identifies which neurons are responding the most and uses this information to determine the pitch. This explanation of the physiology of pitch perception has been called the **place theory**, because it is based on the relation between a sound's frequency and the place along the basilar membrane that is activated.

This explanation is elegant in its simplicity, and it became the standard explanation of the physiology of pitch. Meanwhile, however, some auditory researchers were questioning the validity of place theory. One argument against place was based on the effect of the missing fundamental, in which removing the fundamental frequency of a complex tone does not change the tone's pitch (p. 270). Thus, the tone in Figure 11.6a, which has a fundamental frequency of 200 Hz, has the same pitch after the 200 Hz fundamental is removed, as in Figure 11.6b. What this means is that there is no longer peak vibration at the place associated with 200 Hz.

A modified version of place theory explains this result by considering how the basilar membrane vibrates to complex tones. Figure 11.28 shows that a complex tone causes peaks in vibration for the fundamental (200 Hz) and for each harmonic. Thus, removing the fundamental eliminates the peak at 200 Hz, but peaks would remain at 400, 600, and 800, and this pattern of places, spaced 200 Hz apart, matches the fundamental frequency so can be used to determine the pitch.

As it turns out, however, the idea that pitch can be determined by harmonics, as in **Figure 11.28**, works only for low harmonics—harmonics that are close to the fundamental. We can see why this is so by considering the tone with fundamental



(a) **Frequency spectrum** (b) **Basilar membrane**

Figure 11.28 (a) Frequency spectrum for a complex tone with fundamental frequency 200 Hz, showing the fundamental and three harmonics. (b) Basilar membrane. The shaded areas indicate approximate locations of peak vibration associated with each harmonic in the complex tone.

frequency of 440 Hz shown in **Figure 11.29a**. **Figure 11.29b** shows the cochlear filter banks which correspond to frequency tuning curves like the ones in Figure 11.25. When the 440 Hz tone is presented, it most strongly activates the filter highlighted in red and the 880 Hz second harmonic is highlighted in green.

Now let's move up to higher harmonics. The 5,720-Hz 13th harmonic and the 6,160-Hz 14th harmonic both activate the two overlapping filters highlighted in purple. This means

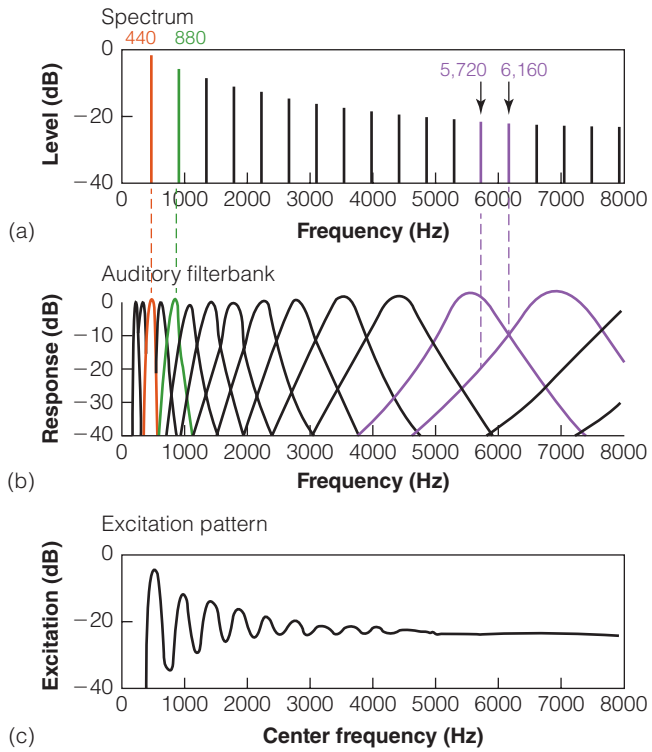


Figure 11.29 (a) Frequency spectrum for the first 18 harmonics for a tone with 440-Hz fundamental frequency. (b) Cochlear filter bank. Note that the filters are narrower at lower frequencies. The red filter is activated by the 440-Hz harmonic; the green one by the 880-Hz harmonic; the purple ones by the 5,720- and 6,160-Hz harmonics. The filters correspond to the frequency tuning curves of cochlear nerve fibers like the ones shown in Figure 11.25. (c) Excitation pattern on the basilar membrane, which shows individual peaks of vibration for the early (resolved) harmonics and no peaks for the later (unresolved) harmonics. (Adapted from Oxenham, 2013)

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that lower harmonics activate separated filters while high harmonics can activate the same filters. Taking the properties of the filter bank into account results in the excitation curve in **Figure 11.29c**, which is essentially a picture of the amplitude of basilar membrane vibration caused by each of the tone's harmonics (Oxenham, 2013).

What stands out about the excitation curve is that the tone's lower harmonics each cause a distinct bump in the excitation curve. Because each of these lower harmonics can be distinguished by a peak, they are called **resolved harmonics**, and frequency information is available for perceiving pitch. In contrast, the excitations caused by the higher harmonics create a smooth function that doesn't indicate the individual harmonics. These higher harmonics are called **unresolved harmonics**.

What's important about resolved and unresolved harmonics is that a series of resolved harmonics results in a strong perception of pitch, but unresolved harmonics result in a weak perception of pitch. Thus, a tone with the spectral composition 400, 600, 800, and 1,000 Hz results in a strong perception of pitch corresponding to the 200-Hz fundamental. However, the smeared out pattern that would be caused by higher harmonics of the 200 Hz fundamental, such as 2,000, 2,200, 2,400, and 2,600 Hz results in a weak perception of pitch corresponding to 200 Hz. What this all means is that place information provides an incomplete explanation of pitch perception.

In addition to the fact that unresolved harmonics result in poor pitch perception, other research revealed other phenomena that were difficult for even this modified version of place theory to explain. Edward Burns and Neal Viemeister (1976) created a sound stimulus that wasn't associated with vibration of a particular place on the basilar membrane, but which created a perception of pitch. This stimulus was called **amplitude-modulated noise**. **Noise** is a stimulus that contains many random frequencies so it doesn't create a vibration pattern on the basilar membrane that corresponds to a specific frequency. **Amplitude modulation** means that the level (or intensity) of the noise was changed so the loudness of the noise fluctuated rapidly up and down.

Burns and Viemeister found that this noise stimulus resulted in a perception of pitch, which they could change by varying the rate of the up-and-down changes in level. The conclusion from this finding, that pitch can be perceived even in the absence of place information, has been demonstrated in a large number of experiments using different types of stimuli (Oxenham, 2013; Yost, 2009).

Temporal Information and Pitch

If place isn't the answer, what is? One way to answer this question is to look back at Figure 11.6 and note what happens when the 200-Hz fundamental frequency is removed. Notice that although the waveform of the tone changes, the timing, or repetition rate, remains the same. Thus, there is information in the timing of a tone stimulus that is associated with the tone's pitch. We also saw that this timing occurs in the neural response to a tone because of phase locking.

When we discussed phase locking on page 276, we saw that because nerve fibers fire at the same time in the sound stimulus, the sound produces a pattern of nerve firing in groups of neurons that matches the frequency of the sound stimulus (Figure 11.20). Thus, the timing of firing of groups of neurons provides information about the fundamental frequency of a complex tone, and this information exists even if the fundamental frequency or other harmonics are absent.

The reason phase locking has been linked to pitch perception is that pitch perception occurs only for frequencies up to about 5,000 Hz, and phase locking also occurs only up to 5,000 Hz. The idea that tones have pitch only for frequencies up to 5,000 Hz may be surprising, especially given that the audibility curve (Figure 11.8) indicates that the range of hearing extends up to 20,000 Hz. However, remember from page 270 that pitch is defined as *that aspect of auditory sensation whose variation is associated with musical melodies* (Plack, Barker, & Hall, 2014). This definition is based on the finding that when tones are strung together to create a melody, we only perceive a melody if the tones are below 5,000 Hz (Attneave & Olson, 1971). It is probably no coincidence that the highest note on an orchestral instrument (the piccolo) is about 4,500 Hz. Melodies played using frequencies above 5,000 Hz sound rather strange. You can tell that something is changing but it doesn't sound musical. So it seems that our sense of musical pitch may be limited to those frequencies that create phase locking.

The existence of phase locking below 5,000 Hz, along with other evidence, has led most researchers to conclude that **temporal coding** is the major mechanism of pitch perception.

Problems Remaining to Be Solved

You may, at this point, be getting the idea that there is nothing simple about the physiology of pitch perception. The complexity of the problem of pitch perception is highlighted further by research by Andrew Oxenham and coworkers (2011) in which they asked the question: "Can pitch be perceived for frequencies above 5,000 Hz?" (which, remember, is supposed to be the upper frequency limit for perceiving pitch). They answered this question by showing that if a large number of high-frequency harmonics are presented, participants do, in fact, perceive pitch. For example, when presented with 7,200, 8,400, 9,600, 10,800, and 12,000 Hz, which are harmonics of a tone with 1,200 Hz fundamental frequency, participants perceived a pitch corresponding to 1,200 Hz, which is the spacing between the harmonics (although the perception of pitch was weaker than the perception to lower harmonics). A particularly interesting aspect of this result is that although each harmonic presented alone did not result in perception of pitch (because they are all above 5,000 Hz), pitch was perceived when a number of harmonics were presented together.

This result raises a number of questions. Is it possible that phase locking occurs above 5,000 Hz? Is it possible that some kind of place mechanism is responsible for the pitch Oxenham's participants heard? We don't know the answer to these questions because we don't know what the limits of phase locking

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are in humans. And just to make things even more interesting, it is important to remember that while pitch perception may depend on the information created by vibration of the basilar membrane and by the firing of auditory nerve fibers that are carrying information from the cochlea, pitch perception is not created by the cochlea. It is created by the brain.

11.6 The Physiology of Pitch Perception: The Brain

Remember that vision depends on information in the retinal image but our experience of seeing occurs when this information is transmitted to the cortex. Similarly, hearing depends on information created by the cochlea, but our experience of hearing depends on processing that occurs after signals leave the cochlea. We begin by describing the trip that nerve impulses take as they travel from the auditory nerve to the auditory cortex.

The Pathway to the Brain

Signals generated in the hair cells of the cochlea are transmitted out of the cochlea in nerve fibers of the auditory nerve (refer back to Figure 11.16). The auditory nerve carries the signals generated by the inner hair cells away from the cochlea along the auditory pathway, eventually reaching the auditory cortex, as shown in **Figure 11.30**. Auditory nerve fibers from the cochlea synapse in a sequence of **subcortical structures**—structures below the cerebral cortex. This sequence begins with the **cochlear nucleus** and continues to the **superior olivary nucleus** in the brain stem, the **inferior colliculus** in the midbrain, and the **medial geniculate nucleus** in the thalamus.

From the medial geniculate nucleus, fibers continue to the **primary auditory cortex** in the temporal lobe of the cortex. If you have trouble remembering this sequence of structures, remember the acronym SONIC MG (a very fast sports car), which represents the three structures between the cochlear nucleus and the auditory cortex, as follows: SON = superior olivary nucleus; IC = inferior colliculus; MG = medial geniculate nucleus.

A great deal of processing occurs as signals travel through the subcortical structures along the pathway from the cochlea to the cortex. Processing in the superior olivary nucleus is important for locating sounds because it is here that signals from the left and right ears first meet (indicated by the presence of both red and blue arrows in Figure 11.30). We will discuss how signals from the two ears help us locate sounds in Chapter 12.

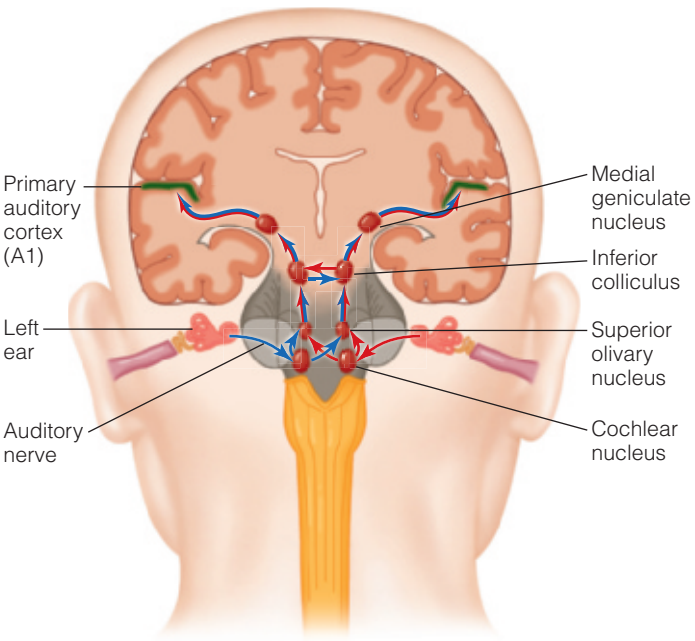

Figure 11.30 Diagram of the auditory pathways. This diagram is greatly simplified, as numerous connections between the structures are not shown. Note that auditory structures are bilateral—they exist on both the left and right sides of the body—and that messages can cross over between the two sides. (Adapted from Wever, 1949)

Pitch and the Brain

Something interesting happens as nerve impulses are traveling up the SONIC MG pathway to the auditory cortex. The temporal information that dominated pitch coding in the cochlea and auditory nerve fibers becomes less important. The main indication of this is that phase locking, which occurred up to about 5,000 Hz in auditory nerve fibers, occurs only up to 100–200 Hz in the auditory cortex (Oxenham, 2013; Wallace et al., 2000). But while temporal information decreases as nerve impulses travel toward the cortex, experiments in the marmoset have demonstrated the existence of individual neurons that seem to be responding to pitch, and experiments in humans have located areas in the auditory cortex that also appear to be responding to pitch.

Pitch Neurons in the Marmoset An experiment by Daniel Bendor and Xiaoqin Wang (2005) determined how neurons in regions partially overlapping the primary auditory cortex of a marmoset (a species of New World monkey) responded to complex tones that differed in their harmonic structure but would be perceived by humans as having the same pitch. When they did this, they found neurons that responded similarly to complex tones with the same fundamental frequency but with different harmonic structures. For example, **Figure 11.31a** shows the frequency spectra for a tone with a fundamental frequency of 182 Hz. In the top record, the tone contains the fundamental frequency and the second and third harmonics; in the second record, harmonics 4–6 are present; and so on, until at the bottom, only harmonics 12–14 are present. Even though these stimuli contain different frequencies (for example, 182, 364, and 546 Hz in the top record; 2,184, 2,366, and 2,548 Hz in the bottom record), they are all perceived by humans as having a pitch corresponding to the 182-Hz fundamental frequency.

The corresponding cortical response records (**Figure 11.31b**) show that these stimuli all caused an increase in firing. To demonstrate that this firing occurred only when information about the 182-Hz fundamental frequency was

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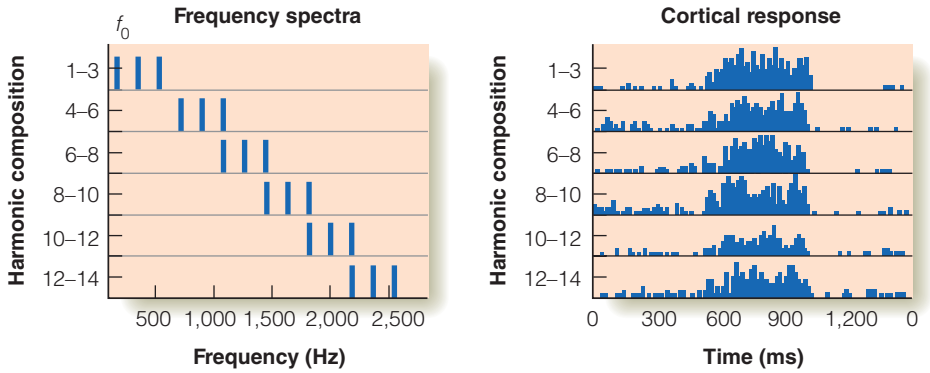

Figure 11.31 Records from a pitch neuron recorded from the auditory cortex of marmoset monkeys. (a) Frequency spectra for tones with a fundamental frequency of 182 Hz. Each tone contains three harmonic components of the 182-Hz fundamental frequency. (b) Response of the neuron to each stimulus. (Adapted from Bendor & Wang, 2005)

present, Bendor and Wang showed that the neuron responded well to a 182-Hz tone presented alone, but not to any of the higher harmonics when they were presented individually. These cortical neurons, therefore, responded only to stimuli associated with the 182-Hz tone, which is associated with a specific pitch. For this reason, Bendor and Wang called these neurons pitch neurons.

Pitch Representation in the Human Cortex

Research on where pitch is processed in the human cortex has used brain scanning (fMRI) to measure the response to stimuli associated with different pitches. This is not as simple as it may seem, because when a neuron responds to sound, this doesn't necessarily mean it is involved in perceiving pitch. To determine whether areas of the brain are responding to pitch, researchers have looked for brain regions that are more active in response to a pitch-evoking sound, such as a complex tone, than to another sound, such as a band of noise that has similar physical features but does not produce a pitch. By doing this, researchers hope to locate brain regions that respond to pitch, irrespective of other properties of the sound.

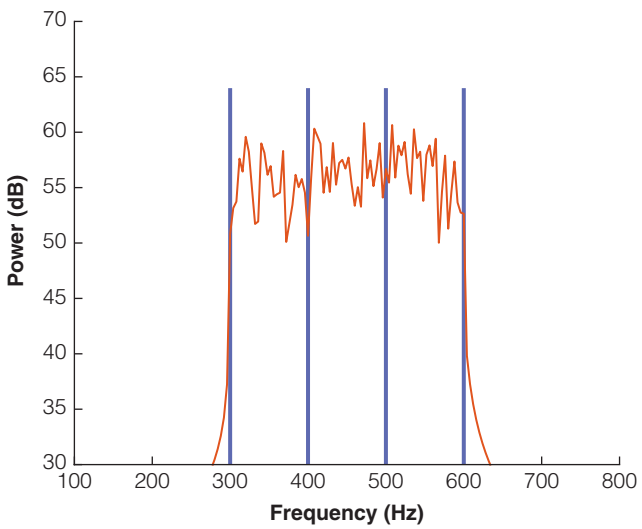

Figure 11.32 Blue: frequency spectra for the 300-, 400-, 500-, and 600-Hz harmonics of a pitch stimulus with fundamental frequency of 100 HZ. Orange: frequency-matched noise, which covers the same range, but without the peaks that produce pitch.

A pitch-evoking stimulus and a noise stimulus used in an experiment by Sam Norman-Haignere and coworkers (2013) are shown in **Figure 11.32**. The pitch stimulus, shown in blue, is the 3rd, 4th, 5th, and 6th harmonics of a complex tone with a fundamental frequency of 100 Hz (300, 400, 500, and 600 Hz); the noise, shown in red, consists of a band of frequencies from 300 to 600 Hz. Because the noise stimulus covers the same range as the pitch stimulus, it is called *frequency-matched noise*.

By comparing fMRI responses generated by the pitch-evoking stimulus to the response from the frequency-matched noise, Norman-Haignere located areas in the primary auditory cortex and some nearby areas that responded more to the pitch-evoking stimulus. The colored areas in **Figure 11.33a** show areas in the human cortex that were tested for their response to pitch. **Figure 11.33b** shows the proportions of fMRI voxels in each area in which the response to the pitch stimulus was greater than the response to the noise stimulus. The areas most responsive to pitch are located in the *anterior auditory cortex*—the area close to the front of the brain. In other experiments, Norman-Haignere determined that the regions that were most responsive to pitch responded to resolved harmonics, but didn't respond as well to unresolved harmonics. Because resolved harmonics are associated with pitch perception, this result strengthens the conclusion that these cortical areas are involved in pitch perception.

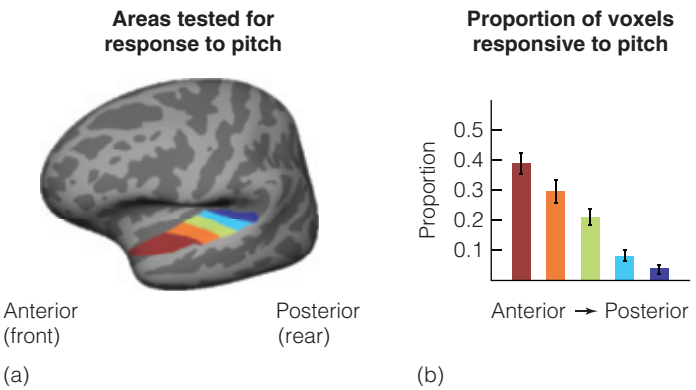

Figure 11.33 (a) Human cortex, showing areas, in color, tested by Norman-Haignere et al. (2013). (b) Graph showing the proportion of voxels in each area that responded to pitch. The more anterior areas (located toward the front of the brain) contained more pitch-responsive voxels.

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As we indicated at the beginning of this discussion, determining areas of the brain that respond to pitch involves more than just presenting tones and measuring responses. Researchers in many laboratories have identified auditory areas in the human that respond to pitch, although the results from different laboratories have varied slightly because of differences in stimuli and procedures. The exact location of the human pitch-responding areas is, therefore, still being discussed (Griffiths, 2012; Griffiths & Hall, 2012; Saenz & Langers, 2014).

Whereas most of the early research on the auditory system focused on the cochlea and auditory nerve, the auditory cortex has become a major focus of recent research. We will consider more research on the brain when we describe the mechanisms responsible for locating sounds in space and for the perceptual organization of sound (Chapter 12) and for how we perceive music (Chapter 13) and speech (Chapter 14).

11.7 Hearing Loss

Roughly 17 percent of the U.S. adult population suffers from some form of impaired hearing (Svirsky, 2017). These losses occur for a number of reasons. One cause of hearing loss is noise in the environment, as the ears are often bombarded with noises such as crowds of people talking (or yelling, if at a sporting event), construction sounds, and traffic noise. Noises such as these are the most common cause of hearing loss. Hearing loss is usually associated with damage to the outer hair cells, and recent evidence indicates that damage to auditory nerve fibers may be involved as well. When the outer hair cells are damaged, the response of the basilar membrane becomes similar to the broad response seen for the dead cochleas examined by Békésy; this results in a loss of sensitivity (inability to hear quiet sounds) and a loss of the sharp frequency tuning seen in healthy ears, as shown in Figure 11.27 (Moore, 1995; Plack et al., 2004). The broad tuning makes it harder for hearing-impaired people to separate out sounds—for example, to hear speech sounds in noisy environments.

Inner hair cell damage can also cause a loss of sensitivity. For both inner and outer hair cells, hearing loss occurs for the frequencies corresponding to the frequencies detected by the damaged hair cells. Sometimes inner hair cells are lost over an entire region of the cochlea (a "dead region"), and sensitivity to the frequencies that normally excite that region of the cochlea becomes much reduced.

Of course, you wouldn't want to purposely damage your hair cells, but sometimes we expose ourselves to sounds that over the long term do result in hair cell damage. One of the things that contributes to hair cell damage is living in an industrialized environment, which contains sounds that contribute to a type of hearing loss called *presbycusis*.

Presbycusis

Presbycusis is caused by hair cell damage resulting from the cumulative effects over time of noise exposure, the ingestion of drugs that damage the hair cells, and age-related degeneration. The loss of sensitivity associated with presbycusis, which is greatest at high frequencies, affects males more severely than females. **Figure 11.34** shows the progression of loss as a function of age. Unlike the visual problem of presbyopia (see Chapter 3, page 45), which is an inevitable consequence of aging, presbycusis is more likely to be caused by factors in addition to aging; people in preindustrial cultures, who have not been exposed to the noises that accompany industrialization or to drugs that could damage the ear, often do not experience large decreases in high-frequency hearing in old age. This may be why males, who historically have been exposed to more workplace noise than females, as well as to noises associated with hunting and wartime, experience a greater presbycusis effect.

Although presbycusis may be unavoidable, since most people are exposed over a long period of time to the everyday sounds of our modern environment, there are situations in which people expose their ears to loud sounds that could be avoided. This exposure to particularly loud sounds results in *noise-induced hearing loss*.

Noise-Induced Hearing Loss

Noise-induced hearing loss occurs when loud noises cause degeneration of the hair cells. This degeneration has been observed in examinations of the cochleas of people who have worked in noisy environments and have willed their ear structures to medical research. Damage to the organ of Corti is

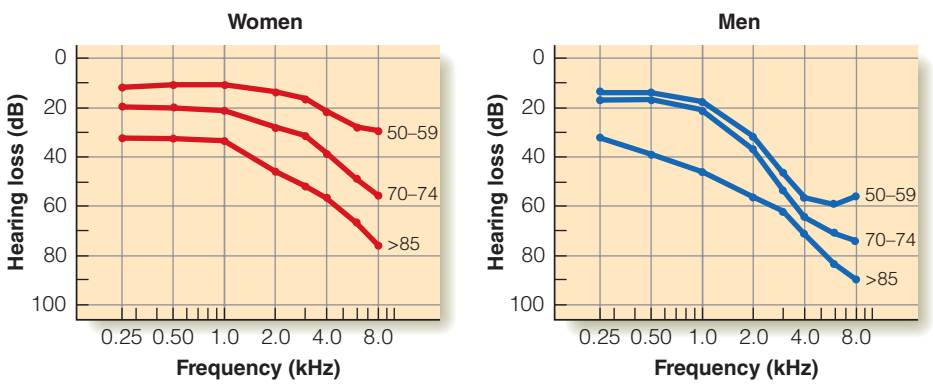

Figure 11.34 Hearing loss in presbycusis as a function of age. All of the curves are plotted relative to the 20-year-old curve, which is taken as the standard. (Adapted from Bunch, 1929)

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often observed in these cases. For example, examination of the cochlea of a man who worked in a steel mill indicated that his organ of Corti had collapsed and no receptor cells remained (Miller, 1974). More controlled studies of animals exposed to loud sounds provide further evidence that high-intensity sounds can damage or completely destroy inner hair cells (Liberman & Dodds, 1984).

Because of the danger to hair cells posed by workplace noise, the United States Occupational Safety and Health Agency (OSHA) has mandated that workers not be exposed to sound levels greater than 85 dB for an 8-hour work shift. In addition to workplace noise, however, other sources of intense sound can cause hair cell damage leading to hearing loss.

If you turn up the volume on your smartphone, you are exposing yourself to what hearing professionals call **leisure noise**. Other sources of leisure noise are activities such as recreational gun use, riding motorcycles, playing musical instruments, and working with power tools. A number of studies have demonstrated hearing loss in people who listen to music with earphones (Okamoto et al., 2011; Peng et al., 2007), play in rock/pop bands (Schmuziger et al., 2006), use power tools (Dalton et al., 2001), and attend sports events (Hodgetts & Liu, 2006). The amount of hearing loss depends on the level of sound intensity and the duration of exposure. Given the high levels of sound that occur in these activities, such as the levels above 90 dB SPL that can occur for the 3 hours of a hockey game (Hodgetts & Liu, 2006), about 100 dB SPL for music venues such as clubs or concerts (Howgate & Plack, 2011), and levels as high as 90 dB SPL while using power tools in woodworking, it isn't surprising that both temporary and permanent hearing losses are associated with these leisure activities. These findings suggest that it might make sense to use ear protection when in particularly noisy environments and to turn down the volume on your phone.

The potential for hearing loss from listening to music at high volume for extended periods of time cannot be overemphasized, because at their highest settings, smartphones reach levels of 100 dB SPL or higher—far above OSHA's recommended maximum of 85 dB. This has led Apple Computer to add a setting to their devices that limits the maximum volume, although an informal survey of my students indicates, not surprisingly, that few of them use this feature.

Hidden Hearing Loss

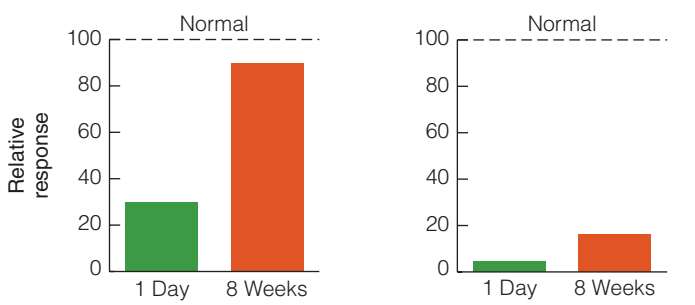
Is it possible to have normal hearing as measured by a standard hearing test, but to have trouble understanding speech in noisy environments? The answer for a large number of people is "yes." People with "normal" hearing who have trouble hearing in noisy environments may be suffering from a recently discovered type of hearing loss called **hidden hearing loss** (Plack, Barker, & Prendergast, 2014). We can understand why this type of hearing loss occurs by considering what the standard hearing test measures.

The standard hearing test involves measuring thresholds for hearing tones across the frequency spectrum. The person sits in a quiet room and is instructed to indicate when he or she hears very faint tones being presented by the tester. The results of this test can be plotted as thresholds covering a range of frequencies—like the audibility curve in Figure 11.8, or as an **audiogram**—a plot of hearing loss versus frequency, like the curves in Figure 11.34. "Normal" hearing is indicated by a horizontal function at 0 dB on the audiogram, indicating no deviation from the normal standard. This hearing test, along with the audiograms it produces, has been called the gold standard of hearing test function (Kujawa & Liberman, 2009).

One reason for the popularity of this test is that it is thought to indicate hair cell functioning. But for hearing complex sounds like speech, especially under noisy conditions such as at a party or in the noise of city traffic, the auditory nerve fibers that transmit signals from the cochlea are also important. Sharon Kujawa and Charles Liberman (2009) determined the importance of having intact auditory nerve fibers through experiments on the effect of noise on hair cells and auditory nerve fibers in the mouse.

Kujawa and Liberman exposed the mice to a 100-dB SPL noise for 2 hours and then measured their hair cell and auditory nerve functioning using physiological techniques we won't describe here. **Figure 11.35a** shows the results for the hair cells, when tested with a 75-dB tone. One day after the noise exposure, hair cell function was decreased below normal (with normal indicated by the dashed line). However, by 8 weeks after the noise exposure, hair cell function had returned almost to normal.

Figure 11.35b shows the response of the auditory nerve fibers to the 75-dB tone. Their function was also decreased right after the noise, but unlike the hair cells, auditory nerve function never returned to normal. The response of nerve fibers to low-level sounds did recover completely, but the response to high-level sounds, like the 75-dB tone, remained below normal. This lack of recovery reflects the fact that the noise exposure had permanently damaged some of the auditory nerve fibers, particularly those that represent information about high sound levels. It is thought that similar effects occur in humans, so that



(a) **Hair cell response** (b) **Auditory nerve response**

Figure 11.35 (a) Mouse hair cell response, as a percentage of normal, to a 75-dB SPL tone following a 2-hour exposure to a 100-dB SPL tone. The response is greatly decreased compared to normal (indicated by the dashed line) 1 day after the exposure but has increased back to normal by 8 weeks after the exposure. (b) The response of auditory nerve fibers is also decreased 1 day after the exposure but fails to recover at 8 weeks, indicating permanent damage. (Based on data from Kujawa & Liberman, 2009)

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even when people have normal sensitivity to low-level sounds and therefore have "clinically normal" hearing, the damaged auditory nerve fibers are responsible for problems hearing speech in noisy environments (Plack, Barker, & Prendergast, 2014).

What is important about this result is that even though some auditory nerve fibers were permanently damaged, the behavioral thresholds to quiet sounds had returned to normal. Thus, a normal audiogram does not necessarily indicate normal auditory functioning. This is why hearing loss due to nerve fiber damage has been described as "hidden" hearing loss (Schaette & McAlpine, 2011). Hidden hearing loss can be lurking in the background, causing serious problems in day-to-day functioning that involves hearing in noisy environments. Further research on hidden hearing loss is focusing on determining what causes it and on developing a test to detect it so this type of hearing loss will no longer be hidden (Plack, Barker, & Prendergast, 2014).

SOMETHING TO CONSIDER:

Explaining Sound to an 11-Year Old

How would you answer the question "What is Sound" in 300 words or less, in a way that would be meaningful to an 11-year-old? That was the assignment for the 2016 edition of the Flame Challenge, which was run by the Alan Alda Center for Communicating Science at Stony Brook University. Given the word limitation and the 11-year-old audience (who voted on the finalists to determine the winner), it's best to minimize technical details and focus on general principles. The entry below, by your author (BG), won first place:

> A drummer bangs on a bass drum. Sam, standing nearby, hears BOOM!
>
> How does banging on the drum turn into the sound BOOM?
>
> Sounds are vibrations, and the drum-head's back-and-forth vibrations create pressure waves in the air that set Sam's eardrums, just inside his ears, into vibration. The magic of sound happens deeper inside Sam's ears in a hollow tube-like structure called the inner ear or cochlea.
>
> Imagine that you've shrunk yourself so small that you can look into this tube. When you peek inside, you see thousands of tiny hairs lined up in rows. Suddenly, the drummer bangs the drum! You feel the vibrations, and then you see something spectacular—the hairs are moving back and forth in time with the vibrations, and every movement is creating electrical signals! These signals are sent down the auditory nerve towards the brain and a fraction of a second later, when they reach the hearing areas in the brain, Sam hears BOOM!
>
> What makes some vibrations create a drum's low-pitched BOOM and others create a bird's high-pitched tweet? Slow vibrations create low pitches and faster vibrations create high pitches, so the hairs vibrate more slowly for BOOM and faster for *tweet*.
>
> But sound is more than BOOM and *tweet*. You create sounds when talking with friends or playing music. Music is really amazing, because when the tiny hairs vibrate back and forth to music, electricity reaches the brain's hearing areas, plus other brain areas that make you move and that make you feel emotions like happy or sad.
>
> So sounds are vibrations that make you hear, and might also make you feel like tapping your feet, dancing, crying, or even jumping for joy. Pretty amazing, what tiny hairs vibrating inside the ear can do!

The Flame Challenge poses different questions each year. How would you answer the question for 2014, "What is Color?"

DEVELOPMENTAL DIMENSION Infant Hearing

What do newborn infants hear, and how does hearing develop as infants get older? Although some early psychologists believed that newborns were functionally deaf, recent research has shown that newborns do have some auditory capacity and that this capacity improves as the child gets older (Werner & Bargones, 1992).

Thresholds and the Audibility Curve

What do infant audibility curves look like, and how do their thresholds compare to adults'? Lynne Werner Olsho and coworkers (1988) used the following procedure to determine infants' audibility curves: An infant is fitted with earphones and sits on the parent's lap. An observer, sitting out of view of the infant, watches the infant through a window. A light blinks on, indicating that a trial has begun, and a tone is either presented or not. The observer's task is to decide whether the infant heard the tone (Olsho et al., 1987).

How can observers tell whether the infant has heard a tone? They decide by looking for responses such as eye movements, changes in facial expression, a wide-eyed look, a turn of the head, or changes in activity level. These judgments resulted in the curve in **Figure 11.36a** for a 2,000-Hz tone (Olsho et al., 1988). Observers only occasionally indicated that the 3-month-old infants had heard a tone that was presented at low intensity or not at all; observers were more likely to say that the infant had heard the tone when the tone was presented at high intensity. The infant's threshold was determined from

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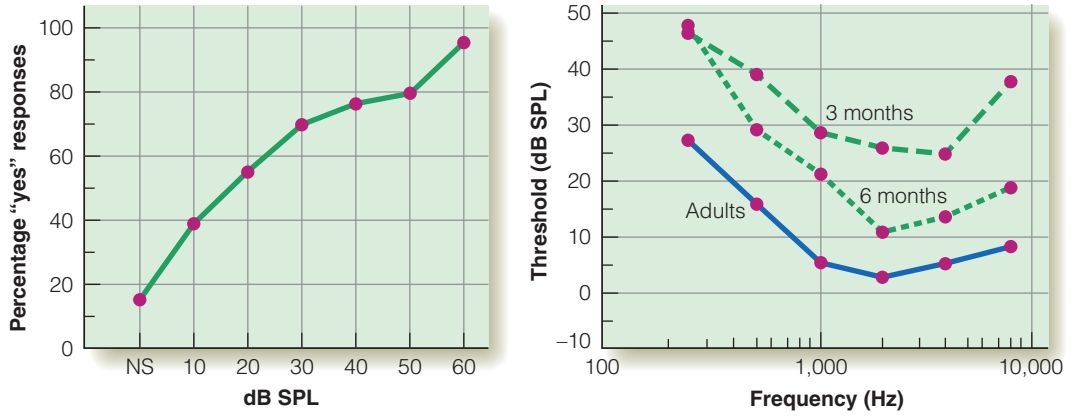

Figure 11.36 (a) Data obtained by Olsho et al. (1987), showing the percentage of trials on which the observer indicated that a 3-month-old infant had heard 2,000-Hz tones presented at different intensities. NS indicates no sound. (b) Audibility curves for 3- and 6-month-old infants determined from functions like the one in (a). The curve for 12-month-olds, not shown here, is similar to the curve for 6-month-olds. The adult curve is shown for comparison. (Adapted from Olsho et al., 1988)

this curve, and the results from a number of other frequencies were combined to create audibility functions such as those in **Figure 11.36b**. The curves for 3- and 6-month-olds and adults indicate that infant and adult audibility functions look similar and that by 6 months of age the infant's threshold is within about 10 to 15 dB of the adult threshold.

Recognizing Their Mother's Voice

Another approach to studying hearing in infants has been to show that newborns can identify sounds they have heard before. Anthony DeCasper and William Fifer (1980) demonstrated this capacity in newborns by showing that 2-day-old infants will modify their sucking on a nipple in order to hear the sound of their mother's voice. They first observed that infants usually suck on a nipple in bursts separated by pauses. They fitted infants with earphones and let the length of the pause in the infant's sucking determine whether the infant heard a recording of the mother's voice or a recording of a stranger's voice (**Figure 11.37**). For half of the infants, long pauses activated the tape of the mother's voice, and short pauses activated the tape of the stranger's voice. For the other half, these conditions were reversed.

Figure 11.37 This baby, from DeCasper and Fifer's (1980) study, could control whether she heard a recording of her mother's voice or a stranger's voice by the way she sucked on the nipple. (From DeCasper & Fifer, 1980)

DeCasper and Fifer found that the babies regulated the pauses in their sucking so that they heard their mother's voice more than the stranger's voice. This is a remarkable accomplishment for a 2-day-old, especially because most had been with their mothers for only a few hours between birth and the time they were tested.

Why did the newborns prefer their mother's voice? DeCasper and Fifer suggested that newborns recognized their mother's voice because they had heard the mother talking during development in the womb. This suggestion is supported by the results of another experiment, in which DeCasper and M. J. Spence (1986) had one group of pregnant women read from Dr. Seuss's book *The Cat in the Hat* and another group read the same story with the words *cat* and *hat* replaced with *dog* and *fog*. When the children were born, they regulated the pauses in their sucking in a way that caused them to hear the version of the story their mother had read when they were in the womb. Moon and coworkers (1993) obtained a similar result by showing that 2-day-old infants regulated their sucking to hear a recording of their native language rather than a foreign language (see also DeCasper et al., 1994).

The idea that fetuses become familiar with the sounds they hear in the womb was supported by Barbara Kisilevsky and coworkers (2003), who presented loud (95-dB) recordings of the mother reading a 2-minute passage and a stranger reading a 2-minute passage through a loudspeaker held 10 cm above the abdomen of full-term pregnant women. When they measured the fetus's movement and heart rate as these recordings were being presented, they found that the fetus moved more in response to the mother's voice, and that heart rate increased in response to the mother's voice but decreased in response to the stranger's voice. Kisilevsky concluded from these results that fetal voice processing is influenced by experience, just as the results of earlier experiments had suggested (see also Kisilevsky et al., 2009).

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TEST YOURSELF 11.3

1. Describe place theory.
2. How is place theory challenged by the effect of the missing fundamental? How can a modification of place theory explain the effect of the missing fundamental?
3. Describe the Burns and Viemeister experiment, which used amplitude-modulated noise, and its implications for place theory.
4. What is the evidence supporting the idea that pitch perception depends on the timing of auditory nerve firing?
5. What are resolved and unresolved harmonics? What is the connection between resolved harmonics and place theory?
6. What problems do Oxenham et al's. (2011) experiment pose for understanding the physiology of pitch perception?
7. Describe the pathway that leads from the ear to the brain.
8. Describe the experiments that suggest a relationship between the firing of neurons in the auditory cortex and the pitch of complex tones in (a) the marmoset and (b) humans.
9. What is the connection between hair cell damage and hearing loss? Exposure to occupational or leisure noise and hearing loss?
10. What is hidden hearing loss?
11. How would you summarize the main point of the essay on "What is Sound," which was written for 11-year olds, in one or two sentences?
12. Describe the procedures for measuring auditory thresholds in infants. How does the infant's audibility curve compare to the adult curve?
13. Describe experiments that show that newborn infants can recognize their mother's voice, and that this capacity can be traced to the infants' having heard the mother talking during development in the womb.

THINK ABOUT IT

1. We saw that decibels are used to compress the large range of sound pressures in the environment into more manageable numbers. Describe how this same principle is used in the Richter scale to compress the range of earth vibrations from barely perceptible tremors to major earthquakes into a smaller range of numbers.
2. Presbycusis usually begins with loss of high-frequency hearing and gradually involves lower frequencies. From what you know about cochlear function, can you explain why the high frequencies are more vulnerable to damage? (p. 284)

KEY TERMS

Amplitude (p. 265)
Amplitude modulation (p. 281)
Amplitude-modulated noise (p. 281)
Aperiodic sound (p. 271)
Apex (of the cochlea or basilar membrane) (p. 277)
Attack (p. 271)
Audibility curve (p. 269)
Audiogram (p. 285)
Auditory canal (p. 272)
Auditory response area (p. 269)
Base (of the cochlea or basilar membrane) (p. 277)
Basilar membrane (p. 274)
Characteristic frequency (p. 278)
Cochlea (p. 273)
Cochlear amplifier (p. 279)
Cochlear nucleus (p. 282)
Cochlear partition (p. 273)
Decay (p. 271)
Decibel (dB) (p. 266)
Eardrum (p. 272)
Effect of the missing fundamental (p. 270)
Equal loudness curve (p. 269)
First harmonic (p. 268)
Frequency (p. 265)
Frequency spectra (p. 268)
Frequency tuning curve (p. 278)
Fundamental (p. 268)
Fundamental frequency (p. 268)
Hair cells (p. 274)
Harmonic (p. 268)
Hertz (Hz) (p. 266)
Hidden hearing loss (p. 285)
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Someone sitting at a riverside table along the San Antonio Riverwalk could be hearing sounds created by conversations with others, passing boats, and music from the restaurants' loudspeakers. Despite this complexity of sounds in the environment, our auditory system is able to determine where sounds are coming from and to separate sounds that are created by different sources.

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Learning Objectives

After studying this chapter, you will be able to ...

- Describe experiments that show how people use different cues to determine the location of a sound source.
- Describe the physiological processes that are involved in determining the location of a sound source.
- Understand how our perception of sound location is determined when listening to sounds inside a room.
- Understand how auditory scene analysis describes how we separate different sound sources that are occurring simultaneously in the environment.
- Describe a number of ways hearing and vision interact in the environment.
- Describe interconnections between vision and hearing in the brain.

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CHAPTER 12

Hearing in the Environment

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TEST YOURSELF 12.2

THINK ABOUT IT

Some Questions We Will Consider:

- What makes it possible to tell where a sound is coming from in space? (p. 292)
- Why does music sound better in some concert halls than in others? (p. 301)
- When we are listening to a number of musical instruments playing at the same time, how can we perceptually separate the sounds coming from the different instruments? (p. 302)

The last chapter was focused mainly on laboratory studies of pitch, staying mostly within the inner ear, with a trip to the cortex. This chapter broadens our perception beyond pitch to consider other auditory qualities, most of which depend on higher-order processes. Here are three "scenarios," each of which is relevant to one of the auditory qualities we will discuss.

Scenario 1: Something Suddenly Happens Outside You're walking down the street, lost in thought, although paying enough attention to avoid bumping into oncoming pedestrians. Suddenly, you hear a screech of brakes and a woman screaming. You quickly turn to the right and see that no one was hurt. But how did you know to turn to the right, and where to look? Somehow you could tell where the sound was coming from. This is *sound localization* (p. 292).

Scenario 2: Some Sounds Inside You're inside a deli, which is actually just a small room with a meat counter at one end. You take a number and are waiting your turn as the butcher calls numbers, one by one. Why do you hear each number only once, despite the fact that the sound waves the butcher is producing when he speaks travel multiple paths to reach your ears: (1) a direct path, from his mouth to your ears; and (2) multiple paths involving reflections off of the countertop, the walls, the ceiling, etc. As you will see, what you hear depends mainly on sound reaching your ears along the first path, a phenomenon called the *precedence effect* (p. 300).

Scenario 3: A Conversation With a Friend You're sitting in a coffee shop, talking with a friend. But there are many other sounds as well—other people talking nearby, the occasional screech of the espresso machine, music from a speaker overhead, a car jams on its brakes outside. How you can separate the sounds your friend is speaking from all the other sounds in the room? The ability to separate each of the sound sources and separate them in space is achieved by a process

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called *auditory stream analysis* (p. 302). While all this is going on, you are able to hear what your friend is saying word by word, and to group her words together to create sentences. This is *perceptual grouping* (p. 303).

This chapter considers each of these situations. We begin by describing mechanisms that enable us to determine where sound is coming from (Scenario 1). We then consider the mechanisms that help us not be confused by sound waves that are bouncing off the walls of a room, with a side-trip to consider architectural acoustics (Scenario 2). We then move on to auditory scene analysis, which involves perceptually separating and arranging sounds in auditory space and grouping sounds coming from a single source (Scenario 3).

Every sound comes from someplace. This may sound like an obvious statement because, of course, something, with a specific location, must be producing each sound. But while we often pay attention to where visible objects are, because they may be destinations to reach, things to avoid, or scenes to observe, we often pay less attention to where sounds are coming from. But locating the sources of sounds, especially ones that might signal danger, can be important for our survival. And even though most sounds don't signal danger, sounds and their locations are constantly structuring our auditory environment. In this section, we describe how you are able to extract information that indicates the location of a sound's source, and how the brain uses this information to create a neural representation of sounds in space.

12.1 Sound Source Localization

Let's begin by making an observation. Close your eyes for a moment, listen, and notice what sounds you hear and where they are coming from. This works best if you aren't in a totally quiet environment!

The results of my observation, sitting in a coffee shop, revealed multiple sounds, coming from different locations. I hear the beat and vocals of a song coming from a speaker above my head and slightly behind me, a woman talking somewhere in front of me, and the "fizzy" sound of an espresso maker off to the left.

I hear each of the sounds—the music, the talking, and the mechanical fizzing sound, as coming from different locations in space. These sounds at different locations create an **auditory space**, which exists all around, wherever there is sound. The locating of sound sources in auditory space is called **auditory localization**. We can appreciate the problem the auditory system faces in determining these locations by comparing the information for location for vision and hearing.

Consider the tweeting bird and the meowing cat in **Figure 12.1**. Visual information for the relative locations of the bird and the cat is contained in the images of the bird and the cat on the surface of the retina. The ear, however, is different. The bird's "tweet, tweet" and the cat's "meow" stimulate the cochlea based on their sound frequencies, and as we saw

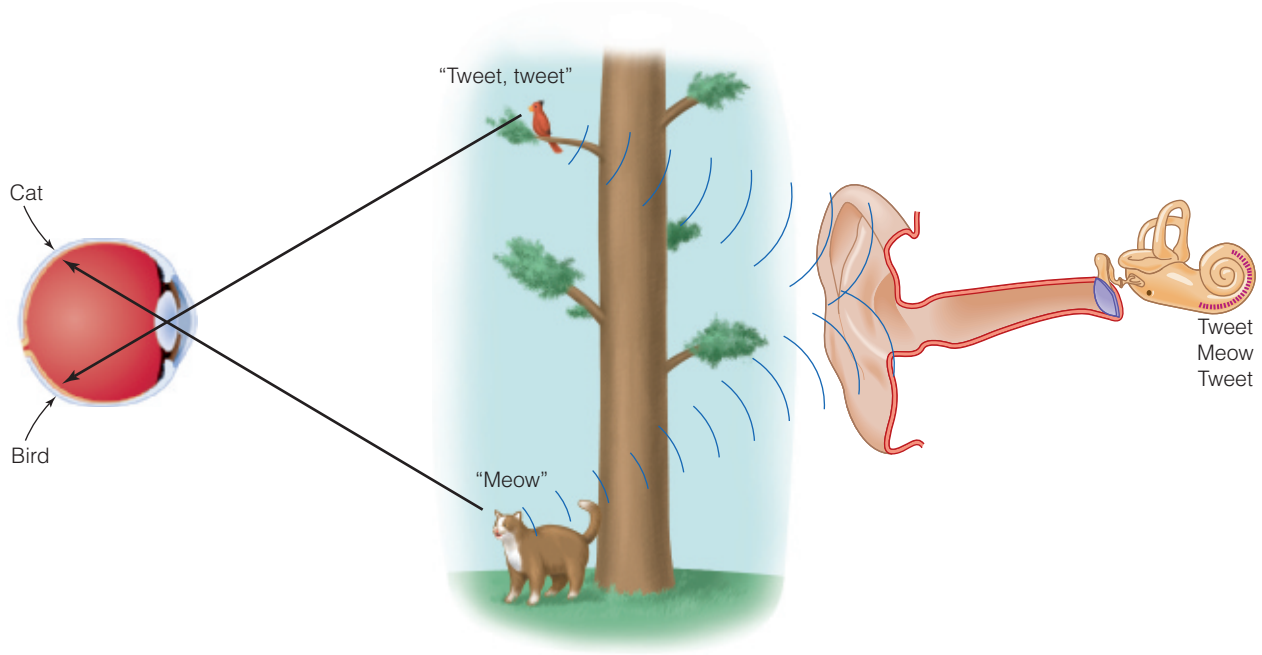

Figure 12.1 Comparing location information for vision and hearing. *Vision:* The bird and the cat, which are located at different places, are imaged on different places on the retina. *Hearing:* The frequencies in the sounds from the bird and cat are spread out over the cochlea, with no regard to the animals' locations.

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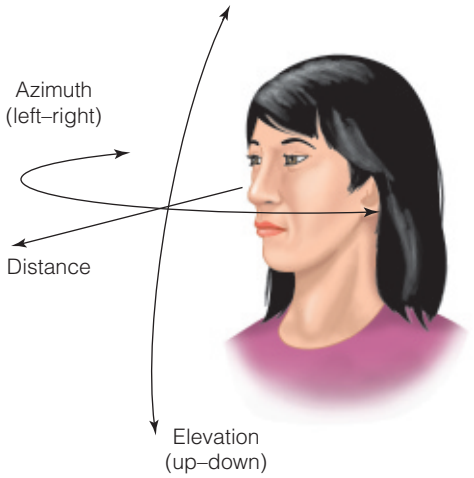

Figure 12.2 The three directions used for studying sound localization: azimuth (left–right), elevation (up–down), and distance.

in Chapter 11, these frequencies cause patterns of nerve firing that result in our perception of a tone's pitch and timbre. But activation of nerve fibers in the cochlea is based on the tones' frequency components and not on where the tones are coming from. This means that two tones with the same frequency that originate in different locations will activate the same hair cells and nerve fibers in the cochlea. The auditory system must therefore use information other than the place on the cochlea to determine location. This information takes the form of location cues that are created by the way sound interacts with the listener's head and ears.

There are two kinds of location cues: *binaural cues*, which depend on both ears, and *spectral cues*, which depend on just one ear. Researchers studying these cues have determined how well people can utilize these cues to locate the position of a sound in three dimensions: the azimuth, which extends from left to right (**Figure 12.2**); elevation, which extends up and down; and the distance of the sound source from the listener. Localization in distance is much less accurate than azimuth or elevation localization, working best when the sound source is familiar, or when cues are available from room reflections. In this chapter, we will focus on the azimuth and elevation.

Binaural Cues for Sound Localization

Binaural cues use information reaching both ears to determine the azimuth (left–right position) of sounds. The two binaural cues are *interaural level difference* and *interaural time difference*. Both are based on a comparison of the sound signals reaching the left and right ears. Sounds that are off to the side are more intense at one ear than the other and reach one ear before the other.

Interaural Level Difference

Interaural level difference (ILD) is based on the difference in the sound pressure level (or just "level") of the sound reaching the two ears. A difference in level between the two ears occurs because the head is a barrier that creates an acoustic shadow, reducing the intensity of sounds that reach the far ear. This reduction of intensity at the far ear occurs for high-frequency sounds (greater than about 3,000 Hz for humans), as shown in **Figure 12.3a**, but not for low-frequency sounds, as shown in **Figure 12.3b**.

We can understand why an ILD occurs for high frequencies but not for low frequencies by drawing an analogy between sound waves and water waves. Consider, for example, a situation in which small ripples in the water are approaching the boat in **Figure 12.3c**. Because the ripples are small compared to the boat, they bounce off the side of the boat and go no further. Now imagine the same ripples approaching the cattails in **Figure 12.3d**. Because the distance between the ripples is large compared to the stems of the cattails, the ripples are hardly disturbed and continue on their way. These two examples illustrate that an object has a large effect on the wave if it is larger than the distance between the waves (as occurs when short high-frequency sound waves hit the head), but has a small effect if it is smaller than the distance between the waves (as occurs for longer low-frequency sound waves). For this reason, the ILD is an effective cue for location only for high-frequency sounds.

Interaural Time Difference

The other binaural cue, interaural time difference (ITD), is the time difference between when a sound reaches the left ear and when it reaches the right ear (**Figure 12.4**). If the source is located directly in front of the listener, at A, the distance to each ear is the same; the sound reaches the left and right ears simultaneously, so the ITD is zero. However, if a source is located off to the side, at B, the sound reaches the right ear before it reaches the left ear. Because the ITD becomes larger as sound sources are located more to the side, the magnitude of the ITD can be used as a cue to determine a sound's location. Behavioral experiments show that ITD is most effective for determining the locations of low-frequency sounds (Yost & Zhong, 2014) and ILD is most effective for high-frequency sounds, so between them they cover the frequency range for hearing. However, because most sounds in the environment contain low-frequency components, ITD is the dominant binaural cue for hearing (Wightman & Kistler, 1992).

The Cone of Confusion

While the time and level differences provide information that enables people to judge location along the azimuth coordinate, they provide ambiguous information about the elevation of a sound source. You can understand why this is so by imagining you are extending your hand directly in front of you at arm's length and are holding a sound source. Because the source would be equidistant from your left and right ears, the time and level differences would be zero. If you now imagine moving your hand straight up, increasing the sound source's elevation, the source will still be equidistant from the two ears, so both time and level differences are still zero.

Because the time and level differences can be the same at a number of different elevations, they cannot reliably indicate the elevation of the sound source. Similar ambiguous information is provided when the sound source is off to the side.

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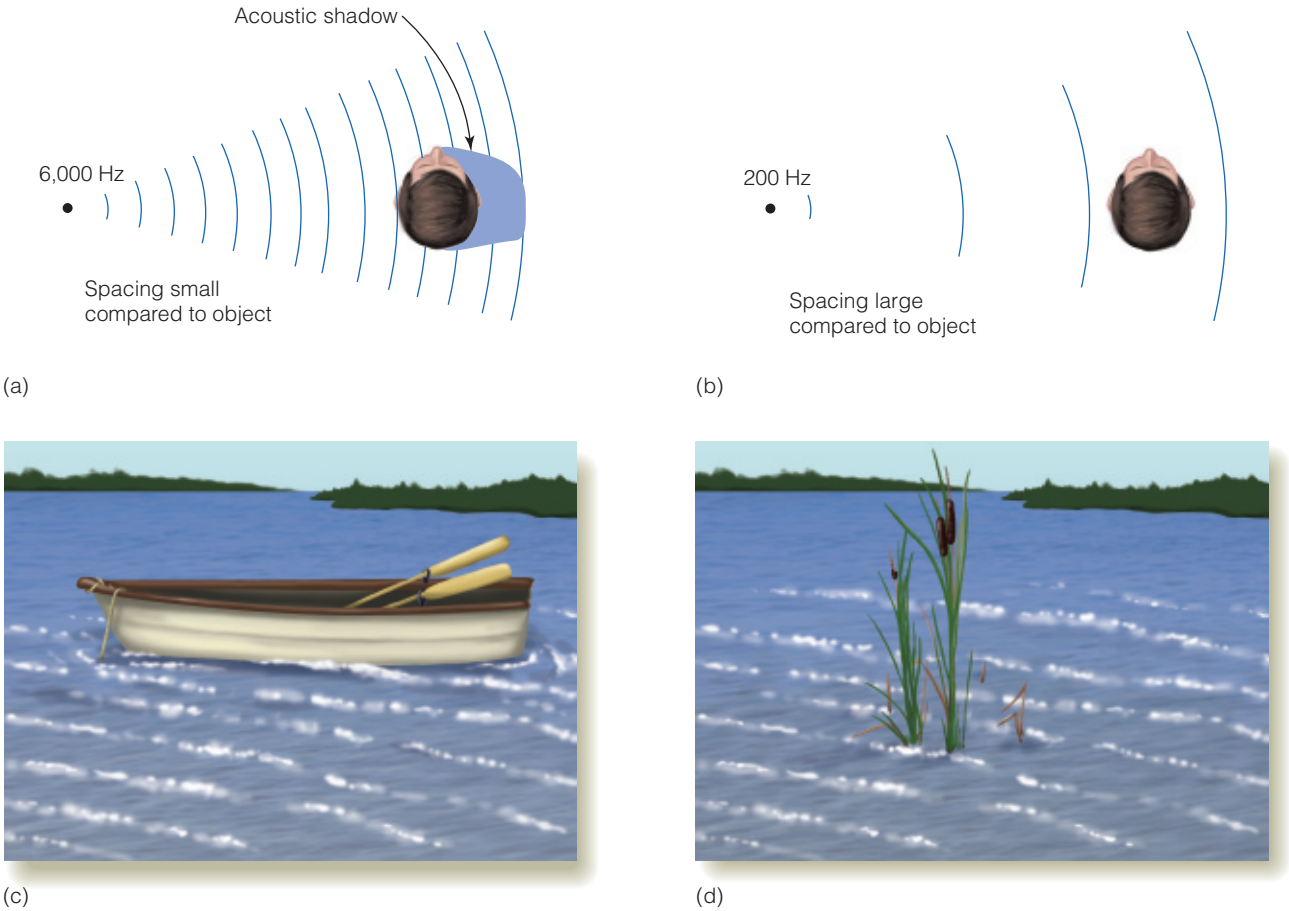

Figure 12.3 Why interaural level difference (ILD) occurs for high frequencies but not for low frequencies. (a) Person listening to a high-frequency sound; (b) person listening to a low-frequency sound. (c) When the spacing between waves is smaller than the size of the object, illustrated here by water ripples that are smaller than the boat, the waves are stopped by the object. This occurs for the high-frequency sound waves in (a) and causes the sound intensity to be lower on the far side of the listener's head. (d) When the spacing between waves is larger than the size of the object, as occurs for the water ripples and the narrow stalks of the cattails, the object does not interfere with the waves. This occurs for the low-frequency sound waves in (b), so the sound intensity on the far side of the head is not affected.

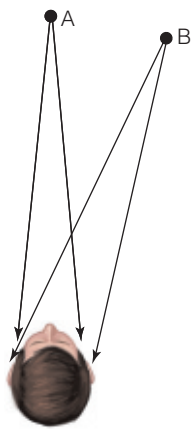

Figure 12.4 The principle behind interaural time difference (ITD). The tone directly in front of the listener, at A, reaches the left and right ears at the same time. However, when the tone is moved to the side, at B, it reaches the listener's right ear before it reaches the left ear.

These places of ambiguity are illustrated by the cone of confusion shown in **Figure 12.5**. All points on the surface of this cone have the same ILD and ITD. For example, points A and B would result in the same ILD and ITD because the distance from A to the left and right ears is the same as the distance from B to the right and left ears. Similar situations occur for other points on the cone, and there are other smaller and larger cones as well. In other words, there are many locations in space where two sounds could result in the same ILD and ITD.

Spectral Cues for Localization

The ambiguous nature of the information provided by the ILD and ITD at different elevations means that another source of information is needed to locate sounds along the elevation coordinate. This information is provided by spectral cues—cues in which information for localization is contained in differences in the distribution (or spectrum) of frequencies that

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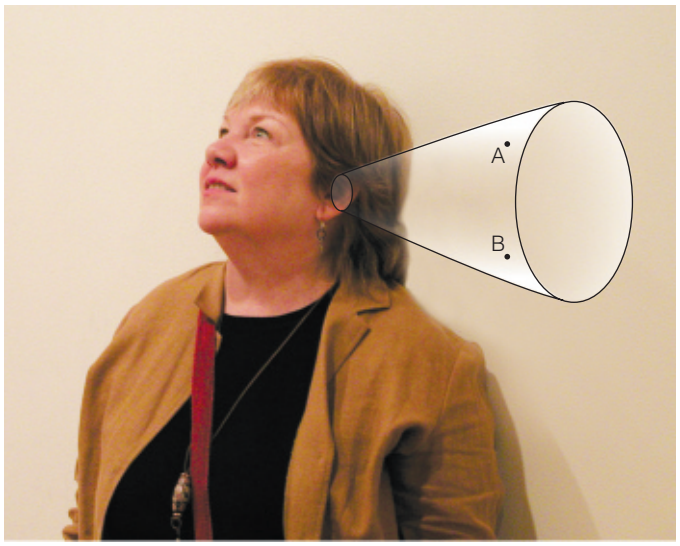

Figure 12.5 The "cone of confusion." There are many pairs of points on this cone that have the same left-ear distance and right-ear distance and so result in the same ITD and ILD. There are also other cones in addition to this one.

reach each ear from different locations. These differences are caused by the fact that before the sound stimulus enters the auditory canal, it is reflected from the head and within the various folds of the pinnae (**Figure 12.6a**). The effect of this interaction with the head and pinnae has been measured by placing small microphones inside a listener's ears and comparing frequencies from sounds that are coming from different directions.

This effect is illustrated in **Figure 12.6b**, which shows the frequencies picked up by the microphone when a broadband sound (one containing many frequencies) is presented at elevations of 15 degrees above the head and 15 degrees below the head. Sounds coming from these two locations would result in the same ILD and ITD because they are the same distance from the left and right ears, but differences in the way the sounds bounce around within the pinna create different patterns of frequencies for the two locations (King et al., 2001). The importance of the pinnae for determining elevation has been demonstrated by showing that smoothing out the nooks and crannies of the pinnae with molding compound makes it difficult to locate sounds along the elevation coordinate (Gardner & Gardner, 1973).

The idea that localization can be affected by using a mold to change the inside contours of the pinnae was also demonstrated by Paul Hofman and coworkers (1998). They determined how localization changes when the mold is worn for several weeks, and then what happens when the mold is removed. The results for one listener's localization performance measured before the mold was inserted are shown in **Figure 12.7a**. Sounds were presented at positions indicated by the intersections of the blue grid. Average localization performance is indicated by the red grid. The overlap between the two grids indicates that localization was fairly accurate.

After measuring initial performance, Hofman fitted his listeners with molds that altered the shape of the pinnae and therefore changed the spectral cue. **Figure 12.7b** shows that localization performance is poor for the elevation coordinate immediately after the mold is inserted, but locations can still be judged at locations along the azimuth coordinate. This is exactly what we would expect if binaural cues are used for judging azimuth location and spectral cues are responsible for judging elevation locations.

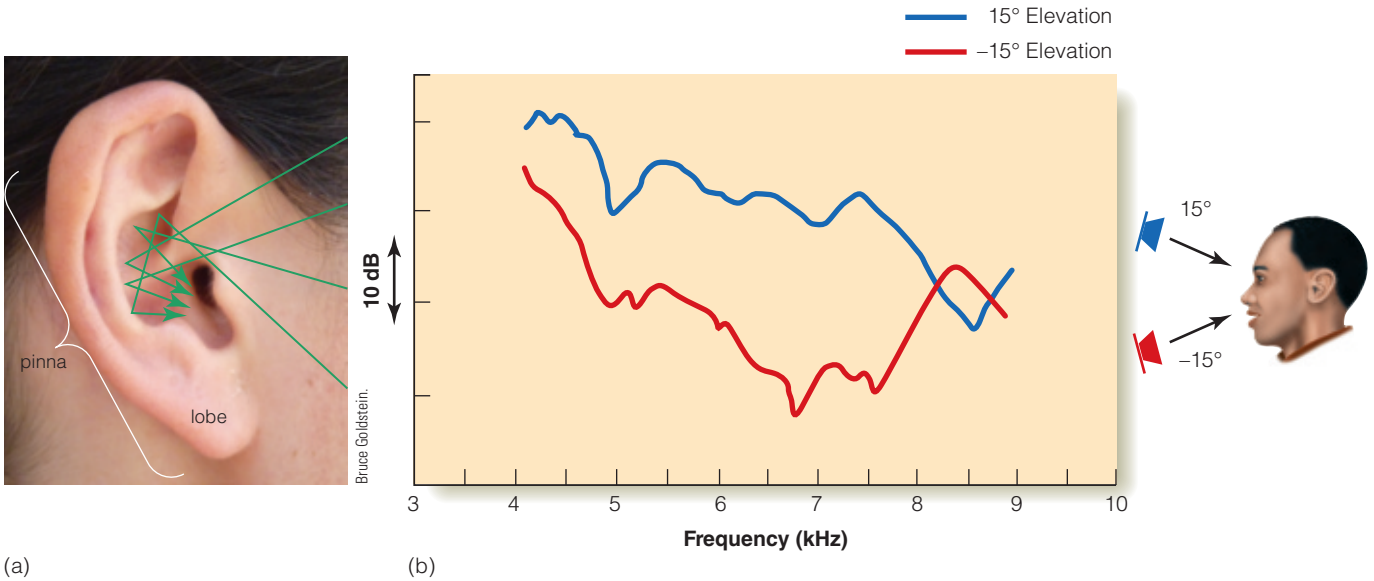

Figure 12.6 (a) Pinna showing sound bouncing around in nooks and crannies. (b) Frequency spectra recorded by a small microphone inside the listener's right ear for the same broadband sound coming from two different locations. The difference in the pattern when the sound is 15 degrees above the head (blue curve) and 15 degrees below the head (red curve) is caused by the way different frequencies bounce around within the pinna when entering it from different angles. (Adapted from Plack, 2005; photo by Bruce Goldstein)

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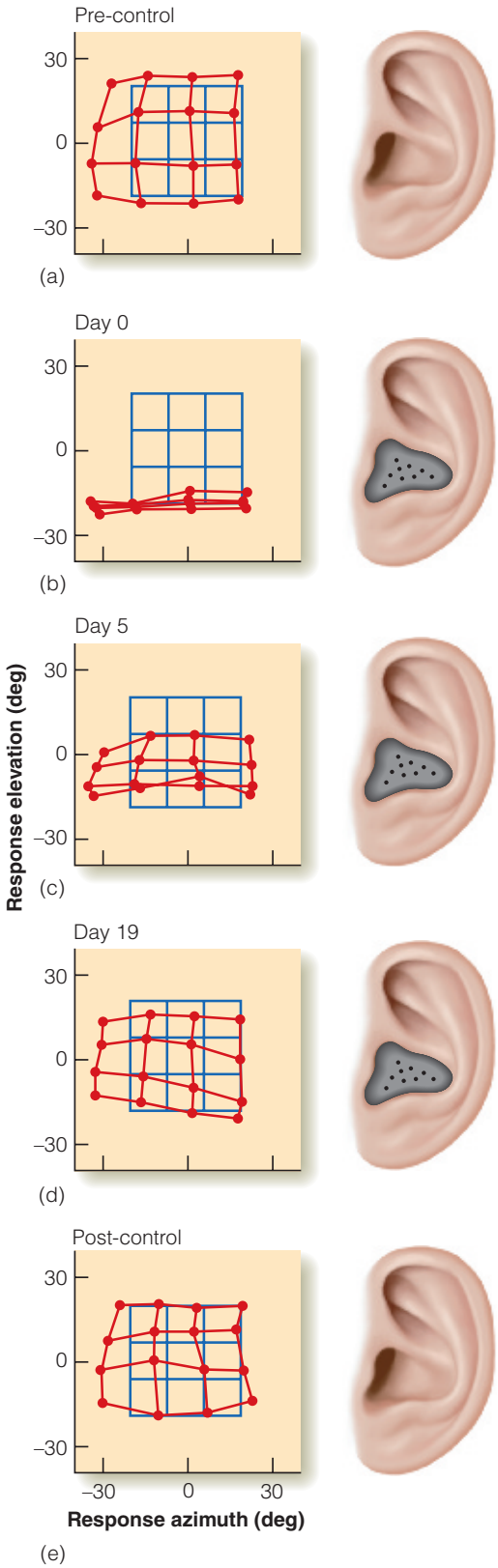

Figure 12.7 How localization changes when a mold is placed in the ear. See text for explanation. (Reprinted from King et al., 2001)

Hofman continued his experiment by retesting localization as his listeners continued to wear the molds. You can see from **Figures 12.7c** and **12.7d** that localization performance improved, until by 19 days localization had become reasonably accurate. Apparently, the person had learned, over a period of weeks, to associate new spectral cues to different directions in space.

What do you think happened when the molds were removed? It would be logical to expect that once adapted to the new set of spectral cues created by the molds, localization performance would suffer when the molds were removed. However, as shown in **Figure 12.7e**, localization remained excellent immediately after removal of the ear molds. Apparently, training with the molds created a new set of correlations between spectral cues and location, but the old correlation was still there as well. One way this could occur is if different sets of neurons were involved in responding to each set of spectral cues, just as separate brain areas are involved in processing different languages in people who have learned a second language as adults (King et al., 2001; Wightman & Kistler, 1998; also see Van Wanrooij & Van Opstal, 2005).

We have seen that each type of cue works best for different frequencies and different coordinates. ILDs and ITDs work for judging azimuth location, with ILD best for high frequencies and ITD for low frequencies. Spectral cues work best for judging elevation, especially for spectra extending to higher frequencies. These cues work together to help us locate sounds. In real-world listening, we also move our heads, which provides additional ILD, ITD, and spectral information that helps minimize the effect of the cone of confusion and helps locate continuous sounds. Vision also plays a role in sound localization, as when you hear talking and see a person making gestures and lip movements that match what you are hearing. Thus, the richness of the environment and our ability to actively search for information help us zero in on a sound's location.

12.2 The Physiology of Auditory Localization

Having identified the cues that are associated with where a sound is coming from, we now ask how the information in these cues is represented in the nervous system. Are there neurons in the auditory system that signal ILD or ITD? Because ITD is the most important binaural cue for most listening situations, we will focus on this cue. We begin by describing a neural circuit that was proposed in 1948 by Lloyd Jeffress to show how signals from the left and right ears can be combined to determine the ITD (Jeffress, 1948; Vonderschen & Wagner, 2014).

The Jeffress Neural Coincidence Model

The Jeffress model of auditory localization proposes that neurons are wired so they each receive signals from the two ears, as shown in **Figure 12.8**. Signals from the left ear arrive along

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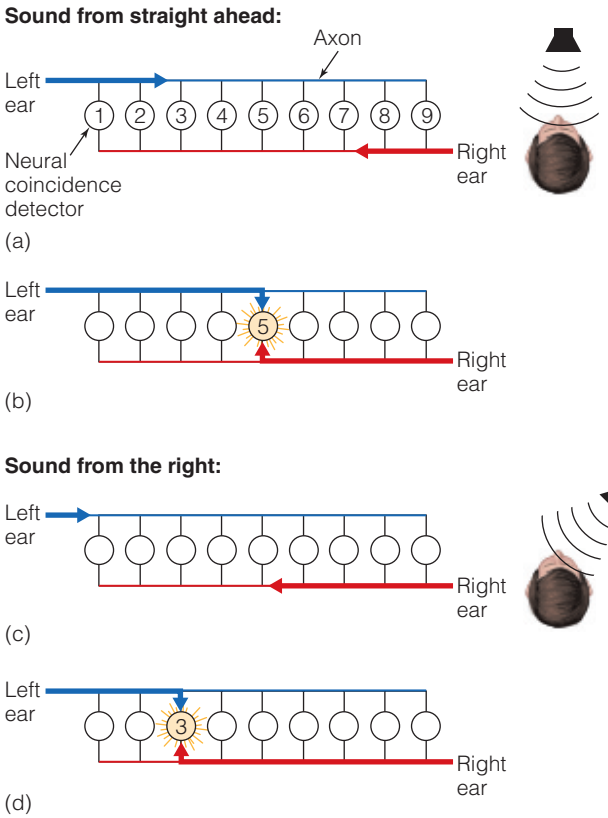

Figure 12.8 How the circuit proposed by Jeffress operates. Axons transmit signals from the left ear (blue) and the right ear (red) to neurons, indicated by circles. (a) Sound in front. Signals start in left and right channels simultaneously. (b) Signals meet at neuron 5, causing it to fire. (c) Sound to the right. Signal starts in the right channel first. (d) Signals meet at neuron 3, causing it to fire. (Adapted from Plack, 2005)

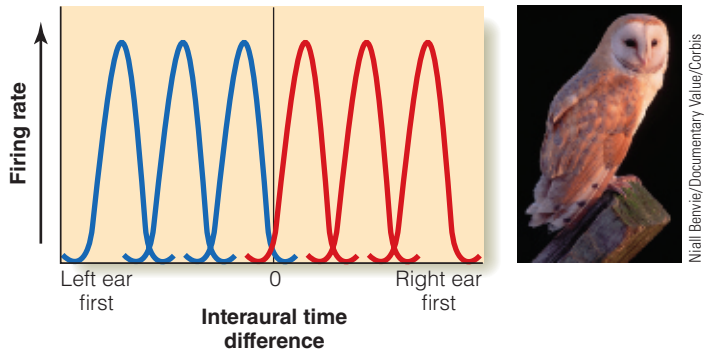

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Figure 12.9 ITD tuning curves for six neurons that each respond to a narrow range of ITDs. The neurons on the left respond when sound reaches the left ear first. The ones on the right respond when sound reaches the right ear first. Neurons such as these have been recorded from the barn owl and other animals. However, when we consider mammals, another story emerges, as illustrated in Figure 12.10. (Adapted from McAlpine & Grothe, 2003)

the blue axon, and signals from the right ear arrive along the red axon.

If the sound source is directly in front of the listener, the sound reaches the left and right ears simultaneously, and signals from the left and right ears start out together, as shown in **Figure 12.8a**. As each signal travels along its axon, it stimulates each neuron in turn. At the beginning of the journey, neurons receive signals from only the left ear (neurons 1, 2, 3) or the right ear (neurons 9, 8, 7), but not both, and they do not fire. But when the signals both reach neuron 5 together, that neuron fires (**Figure 12.8b**). This neuron and the others in this circuit are called coincidence detectors, because they only fire when both signals coincide by arriving at the neuron simultaneously. The firing of neuron 5 indicates that ITD = 0.

If the sound comes from the right, the sound reaches the right ear first, that gives the signal from the right ear a head start, as shown in **Figure 12.8c**, so that it travels all the way to neuron 3 before it meets up with the signal from the left ear. Neuron 3, in this diagram, detects ITDs that occur when the sound is coming from a specific location on the right. The other neurons in the circuit fire to locations corresponding to other ITDs. We can therefore call these coincidence detectors ITD detectors, since each one fires best to a particular ITD.

The Jeffress model therefore proposes a circuit that contains a series of ITD detectors, each tuned to respond best to a specific ITD. According to this idea, the ITD will be indicated by which ITD neuron is firing. This has been called a "place code" because ITD is indicated by the place (which neuron) where the activity occurs.

One way to describe the properties of ITD neurons is to measure ITD tuning curves, which plot the neuron's firing rate against the ITD. Recording from neurons in the brainstem of the barn owl, which has excellent auditory localization abilities, has revealed narrow tuning curves that respond best to specific ITDs, like the ones in **Figure 12.9** (Carr & Konishi, 1990; McAlpine, 2005). The neurons associated with the curves on the left (blue) fire when the sound reaches the left ear first, and the ones on the right (red) fire when sound reaches the right ear first. These are the tuning curves that are predicted by the Jeffress model, because each neuron responds best to a specific ITD and the response drops off rapidly for other ITDs. The place code proposed by the Jeffress model, with its narrow tuning curves, works for owls and other birds, but the situation is different for mammals.

Broad ITD Tuning Curves in Mammals

The results of research in which ITD tuning curves are recorded from mammals may appear, at first glance, to support the Jeffress model. For example, **Figure 12.10** shows an ITD tuning curve of a neuron in the gerbil's superior olivary nucleus (solid line) (see Figure 11.30, page 282) (Pecka et al., 2008). This curve has a peak at an ITD of about 200 microseconds and drops off on either side. However, when we plot the owl curve on the same graph (dashed line) we can see that the gerbil curve is much broader than the owl curve. In fact, the gerbil curve is so broad that it peaks at ITDs far outside the range of ITDs that a gerbil would actually hear in nature, indicated by the light bar (also see Siveke et al., 2006).

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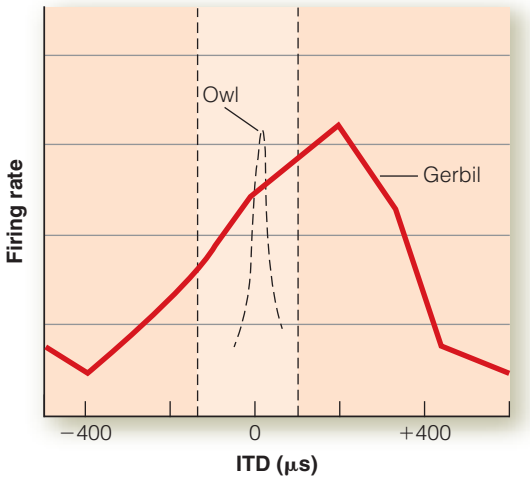

Figure 12.10 Solid curve: ITD tuning curve for a neuron in the gerbil superior olivary nucleus. Dashed curve: ITD tuning curve for a neuron in the barn owl's inferior colliculus. The owl curve appears extremely narrow because of the expanded time scale compared to Figure 12.9. The gerbil curve is broader than the range of ITDs that typically occur in the environment. This range is indicated by the light bar (between the dashed lines).

Because of the broadness of the ITD curves in mammals, it has been proposed that coding for localization is based on broadly tuned neurons like the ones shown in **Figure 12.11a** (Grothe et al., 2010; McAlpine, 2005). According to this idea, there are broadly tuned neurons in the right hemisphere that respond when sound is coming from the left and broadly tuned neurons in the left hemisphere that respond when sound is coming from the right. The location of a sound is indicated by relative responses of these two types of broadly tuned neurons. For example, a sound from the left would cause the pattern of response shown in the left pair of bars in **Figure 12.11b**; a sound located straight ahead, by the middle pair of bars; and a sound to the right, by the far right bars.

This type of coding resembles the population coding we described in Chapter 2, in which information in the nervous system is based on the pattern of neural responding. This is, in fact, how the visual system signals different wavelengths of light, as we saw when we discussed color vision in Chapter 9, in which wavelengths are signaled by the pattern of response of three different cone pigments (Figure 9.13, page 205).

To summarize research on the neural mechanism of binaural localization, we can conclude that it is based on *sharply tuned* neurons for birds and *broadly tuned* neurons for mammals. The code for birds is a *place code* because the ITD is indicated by firing of neurons at a specific place in the nervous system. The code for mammals is a *population code* because the ITD is determined by the firing of many broadly tuned neurons working together. Next, we consider one more piece of the story for mammals, which goes beyond considering how the ITD is coded by neurons to consider how information about localization is organized in the cortex.

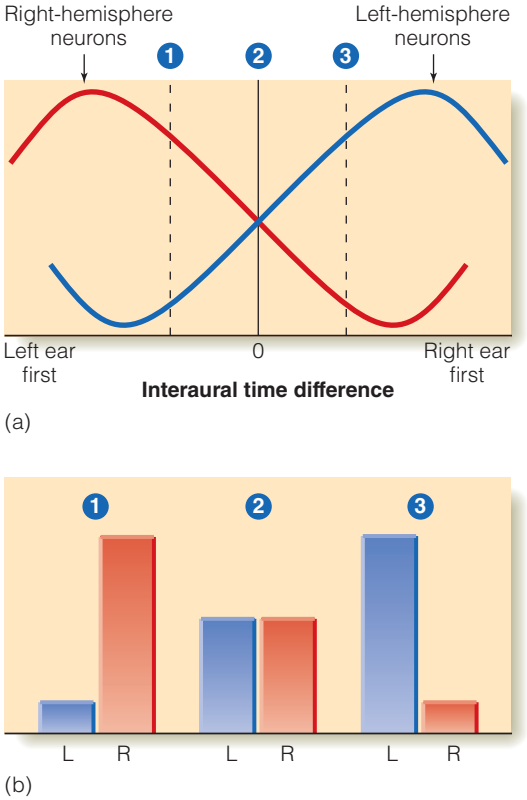

Figure 12.11 (a) ITD tuning curves for broadly tuned neurons like the one shown in Figure 12.10. The left curve represents the tuning of neurons in the right hemisphere; the right curve is the tuning of neurons in the left hemisphere. (b) Patterns of response of the broadly tuned curves for stimuli coming from the left, in front, and from the right. (Adapted from McAlpine, 2005)

Cortical Mechanisms of Localization

The neural basis of binaural localization begins along the pathway from the cochlea to the brain, in the superior olivary nucleus (remember the acronym SONIC MG, that stands for superior olivary nucleus, inferior colliculus, and medial geniculate; see Figure 11.30 page 282), which is the first place that receives signals from the left and right ears. Although a great deal of processing for location occurs as signals are traveling from the ear to the cortex, we will focus on the cortex, beginning with area A1 (**Figure 12.12**).

Area A1 and Locating Sound In a pioneering study, Dewey Neff and coworkers (1956) placed cats about 8 feet away from two food boxes—one about 3 feet to the left, and one about 3 feet to the right. The cats were rewarded with food if they approached the sound of a buzzer located behind one of the boxes. Once the cats learned this localization task, the auditory areas on both sides of the cortex were lesioned (see Method: Brain Ablation, Chapter 4, page 80), and although the cats were then trained for more than 5 months, they were never able to relearn how to localize the sounds. Based on this finding, Neff concluded that an intact auditory cortex is necessary for accurate localization of sounds in space.

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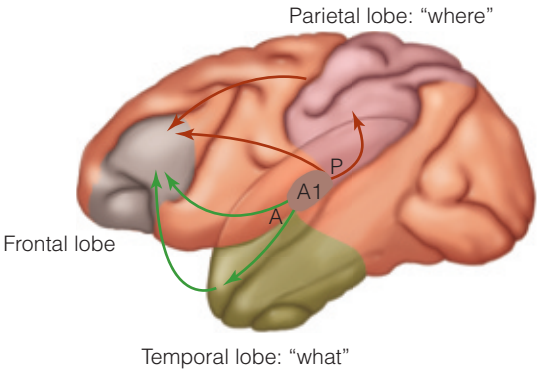

Figure 12.12 Auditory pathways in the monkey cortex. Part of area A1 is visible. The pathways shown here connect to the anterior and posterior belt areas. A = anterior; P = posterior; green = auditory *what* pathway; red = auditory *where* pathway. (Adapted from Rauschecker & Scott, 2009)

Later studies conducted more than 50 years after Neff's research focused more precisely on area A1. Fernando Nodal and coworkers (2010) showed that lesioning the primary auditory cortex in ferrets decreased, but did not totally eliminate, the ferrets' ability to localize sounds. Another demonstration that the auditory cortex is involved in localization was provided by Shveta Malhotra and Stephen Lomber (2007), who showed that deactivating auditory cortex in cats by cooling the cortex results in poor localization (also see Malhotra et al., 2008). These studies of the auditory cortex and localization are summarized in **Table 12.1**.

It is one thing to show that the auditory cortex is involved in localization, but another thing to actually explain how it does it. We know that information about ITD and ILD reaches the cortex. But how is that information combined to create a map of auditory space? We don't know the answer to this question, so research is continuing. One approach to studying localization beyond A1 has focused on the idea that there are two auditory pathways that lead away from A1, called the *what* and *where* auditory pathways.

The *What* and *Where* Auditory Pathways Returning to Figure 12.12, which shows the location of the primary auditory cortex, A1, we can also see two areas labeled A and P on either side of the auditory cortex. A is the **anterior belt area**, and P is the **posterior belt area**. Both of these areas are auditory, but they have different functions. The anterior belt is involved in perceiving complex sounds and patterns of sound and the posterior belt is involved in localizing sounds. Additional research, which we won't describe, has shown that these two parts of the belt are the starting points for two auditory pathways, a ***what* auditory pathway**, which extends from the anterior belt to the front of the temporal lobe and then to the frontal cortex (green arrows in Figure 12.12), and a ***where* auditory pathway**, which extends from the posterior belt to the parietal lobe and then to the frontal cortex (red arrows). The *what* pathway is associated with perceiving sounds and the *where* pathway with locating sounds.

If *what* and *where* pathways sound familiar, it is because we described *what* and *where* pathways for vision in Chapter 4 (see Figure 4.23, page 80). Thus, the idea of pathways serving *what* and *where* functions is a general principle that occurs for both hearing and vision. It is also important to note that although the research we have described is on ferrets, cats, and monkeys, evidence for *what* and *where* auditory functions in humans has been provided by using brain scanning to show that *what* and *where* tasks activate different brain areas in humans (Alain et al., 2001, 2009; De Santis et al., 2007; Wissinger et al., 2001).

We have clearly come a long way from early experiments like Neff's done in the 1950s, which focused on determining the function of large areas of the auditory cortex (p. 298). In contrast, recent experiments have focused on smaller auditory areas and have also shown how auditory processing extends beyond the auditory areas in the temporal lobe to other areas in the cortex. We will have more to say about auditory pathways when we consider speech perception in Chapter 14.

12.3 Hearing Inside Rooms

In this chapter and Chapter 11, we have seen that our perception of sound depends on various properties of the sound, including its frequency, sound level, and location in space. But we have left out the fact that in our normal everyday experience, we hear sounds in a specific setting, such as a small room, a large auditorium, or outdoors. As we consider this aspect of hearing, we will see why we perceive sounds differently when we are outside and inside, and how our perception of sound quality is affected by specific properties of indoor environments.

Figure 12.13 shows how the nature of the sound reaching your ears depends on the environment in which you hear the sound. If you are listening to someone playing a guitar on an outdoor stage, your perception is based mainly on **direct sound**, sound that reaches your ears directly, as shown in **Figure 12.13a**. If, however, you are listening to the same guitar in an auditorium, then your perception is based on direct sound, which reaches your ears directly (path 1), plus **indirect sound**

Table 12.1 Evidence That A1 Is Involved in Localization

REFERENCE	WHAT DONE	RESULT
Neff et al. (1956)	Cat auditory areas destroyed	Localization ability lost
Nodal et al. (2010)	Ferret auditory cortex destroyed	Localization ability decreased
Malhotra & Lomber (2007)	Cat auditory cortex cooled	Localization ability decreased

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(paths 2, 3, and 4), which reaches your ears after bouncing off the auditorium's walls, ceiling, and floor (**Figure 12.13b**).

The fact that sound can reach our ears directly from where the sound is originating and indirectly from other locations creates a potential problem, because even though the sound *originates* in one place, the sound *reaches the listener* from many directions and at slightly different times. This is the situation that we described in Scenario 2 at the beginning of the chapter, in which some of the sound from the butcher's voice reaches the person directly and some reaches the person after bouncing off the walls. We can understand why we usually perceive just one sound, coming from a single location, in situations such as the concert hall or the deli, by considering the results of research in which listeners were presented with sounds separated by time delays, as would occur when they originate from two different locations.

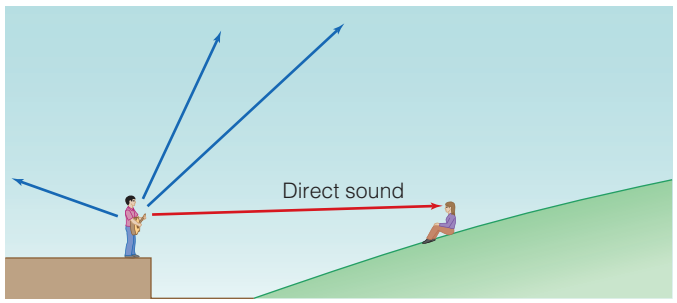
Perceiving Two Sounds That Reach the Ears at Different Times

Research on sound reflections and the perception of location has usually simplified the problem by simulating sound reaching the ears directly from a sound source, followed by a delayed sound from a reflection. This simulation is achieved having people listen to loudspeakers separated in space, as shown in **Figure 12.14**. The speaker on the left is the *lead speaker* (representing the actual sound source), and the one on the right is the *lag speaker* (representing a single sound reflection).

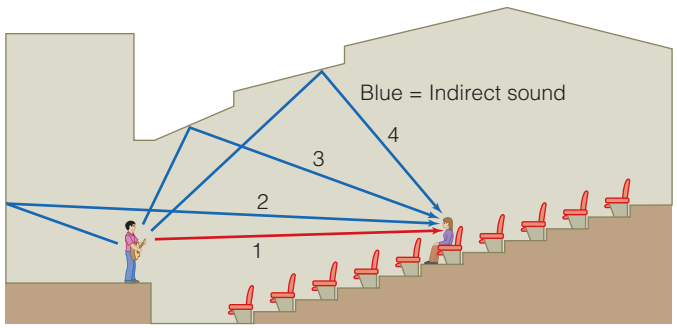
If a sound is presented in the lead speaker followed by a long delay (tenths of a second), and then a sound is presented in the lag speaker, listeners typically hear two separate sounds—one from the left (lead) followed by one from the right (lag) (**Figure 12.14a**). But when the delay between the lead and lag sounds is much shorter, as often occurs in a room, something different happens. Even though the sound is coming from both speakers, listeners hear a single sound as coming only from the lead speaker (**Figure 12.14b**).

This situation, in which a single sound appears to originate from near the lead speaker, is called the **precedence effect** because we perceive the sound as coming from near the source that reaches our ears first (Brown et al., 2015; Wallach et al., 1949). Thus, even though the number called out by the butcher in our *Scenario 2* first reaches the listener's ears directly and is then followed a little later by sound arriving along the indirect path, we just hear his voice once. The point of the precedence effect is that a sound source and its lagging reflections are perceived as a single fused sound, except if the delay is too long, in which case the lagging sounds are perceived as echoes.

The precedence effect governs most of our indoor listening experience. In small rooms, the indirect sounds reflected from the walls have a lower level than the direct sound and reach our ears with delays of about 5 to 10 ms. In larger rooms, like concert halls, the delays are much longer. However, even though our perception of where the sound is coming from is



(a)



(b)

Figure 12.13 (a) When you hear a sound outdoors, sound is radiated in all directions, indicated by the blue arrows, but you hear mainly direct sound, indicated by the red arrow. (b) When you hear a sound inside a room, you hear both direct sound (1) and indirect sound (2, 3, and 4) that is reflected from the walls, floor, and ceiling of the room.

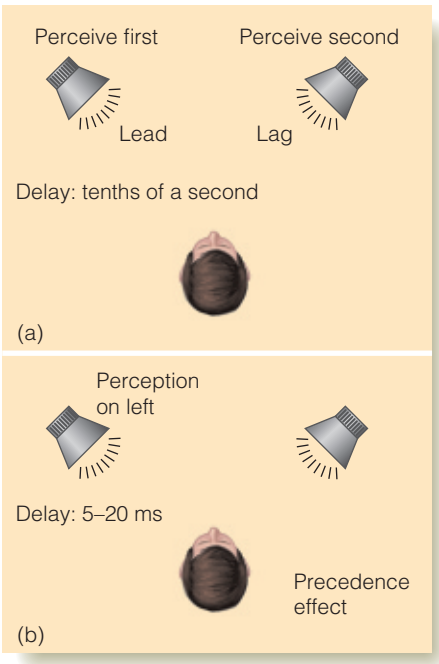


Figure 12.14 (a) When sound is presented first in one speaker and then in the other, with enough time between them, they are heard separately, one after the other. (b) If there is only a short delay between the two sounds, then the sound is perceived to come from the lead speaker only. This is the precedence effect.

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usually determined by the first sound that reaches our ears, the indirect sound, which reaches our ears just slightly later, can affect the *quality* of the sound we hear. The fact that sound quality is determined by both direct and indirect sound is a major concern of the field of architectural acoustics, which is particularly concerned with how to design concert halls.

Architectural Acoustics

Architectural acoustics, the study of how sounds are reflected in rooms, is largely concerned with how indirect sound changes the quality of the sounds we hear in rooms. The major factors affecting indirect sound are the size of the room and the amount of sound absorbed by the walls, ceiling, and floor. If most of the sound is absorbed, then there are few sound reflections and little indirect sound. If most of the sound is reflected, there are many sound reflections and a large amount of indirect sound. Another factor affecting indirect sound is the shape of the room. This determines how sound hits surfaces and the directions in which it is reflected.

The amount and duration of indirect sound produced by a room is expressed as **reverberation time**—the time it takes for the sound to decrease to 1/1000th of its original pressure (or a decrease in level by 60 dB). If the reverberation time of a room is too long, sounds become muddled because the reflected sounds persist for too long. In extreme cases, such as cathedrals with stone walls, these delays are perceived as echoes, and it may be difficult to accurately localize the sound source. If the reverberation time is too short, music sounds "dead," and it becomes more difficult to produce high-intensity sounds.

Because of the relationship between reverberation time and perception, acoustical engineers have tried to design concert halls in which the reverberation time matches the reverberation time of halls that are renowned for their good acoustics, such as Symphony Hall in Boston and the Concertgebouw in Amsterdam, which have reverberation times of about 2.0 seconds. However, an "ideal" reverberation time does not always predict good acoustics. This is illustrated by the problems associated with the design of New York's Philharmonic Hall. When it opened in 1962, Philharmonic Hall had a reverberation time close to the ideal of 2.0 seconds. Even so, the hall was criticized for sounding as though it had a short reverberation time, and musicians in the orchestra complained that they could not hear each other. These criticisms resulted in a series of alterations to the hall, made over many years, until eventually, when none of the alterations proved satisfactory, the entire interior of the hall was destroyed, and in 1992 the hall was completely rebuilt and renamed Avery Fisher Hall. But that's not the end of the story, because even after being rebuilt, the acoustics of Avery Fisher Hall were still not considered adequate. So the hall has been renamed David Geffen Hall, and plans are being discussed regarding the best way to improve its acoustics.

The experience with Philharmonic Hall, along with new developments in the field of architectural acoustics, has led architectural engineers to consider factors in addition to reverberation time in designing concert halls. Some of these factors have been identified by Leo Beranek (1996), who showed that the following physical measures are associated with how music is perceived in concert halls:

- *Intimacy time:* The time between when sound arrives directly from the stage and when the first reflection arrives. This is related to reverberation but involves just comparing the time between the direct sound and the first reflection, rather than the time it takes for many reflections to die down.
- *Bass ratio:* The ratio of low frequencies to middle frequencies that are reflected from walls and other surfaces.
- *Spaciousness factor:* The fraction of all of the sound received by a listener that is indirect sound.

To determine the optimal values for these physical measures, acoustical engineers measured them in 20 opera houses and 25 symphony halls in 14 countries. By comparing their measurements with ratings of the halls by conductors and music critics, they confirmed that the best concert halls had reverberation times of about 2 seconds, but they found that 1.5 seconds was better for opera houses, with the shorter time being necessary to enable people to hear the singers' voices clearly. They also found that intimacy times of about 20 msec and high bass ratios and spaciousness factors were associated with good acoustics (Glanz, 2000). When these factors have been taken into account in the design of new concert halls, such as the Walt Disney Concert Hall in Los Angeles, the result has been acoustics rivaling the best halls in the world.

In designing Walt Disney Hall, the architects paid attention not only to how the shape, configuration, and materials of the walls and ceiling would affect the acoustics, but also to the absorption properties of the cushions on each of the 2,273 seats. One problem that often occurs in concert halls is that the acoustics depend on the number of people attending a performance, because people's bodies absorb sound. Thus, a hall with good acoustics when full could echo when there are too many empty seats. To deal with this problem, the seat cushions were designed to have the same absorption properties as an "average" person. This means that the hall has the same acoustics when empty or full. This is a great advantage to musicians, who usually rehearse in an empty hall.

Another concert hall with exemplary acoustics is the Leighton Concert Hall in the DeBartolo Performing Arts Center at the University of Notre Dame, which opened in 2004 (**Figure 12.15**). The innovative design of this concert hall features an adjustable acoustic system that makes it possible to adjust the reverberation to between 1.4 and 2.6 seconds. This is achieved by motors that control the position of the canopy over the stage and various panels and banners throughout the hall. These adjustments make it possible to "tune" the hall for different kinds of music, so short reverberation times can be achieved for singing and longer reverberation times for orchestral music.

Having considered how we tell where sounds are coming from, how we can make sense of sounds even when they are bouncing around in rooms, and how characteristics of a room can affect what we hear, we are now ready to take the next step in understanding how we make sense of sounds in

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Matt Cashore/University of Notre Dame

Figure 12.15 Leighton Concert Hall in the DeBartolo Performing Arts Center at the University of Notre Dame. Reverberation time can be adjusted by changing the position of the panels and banners on the ceiling and draperies on the sides.

the environment by considering how we perceptually organize sounds when there are many sound sources.

TEST YOURSELF 12.1

1. How is auditory space described in terms of three coordinates?
2. What is the basic difference between determining the location of a sound source and determining the location of a visual object?
3. Describe the binaural cues for localization. Indicate the frequencies and directions relative to the listener for which the cues are effective.
4. Describe the spectral cue for localization.
5. What happens to auditory localization when a mold is placed in a person's ear? How well can a person localize sound once he or she has adapted to the mold? What happens when the mold is removed after the person has adapted to it?
6. Describe the Jeffress model, and how neural coding for localization differs for birds and for mammals.
7. Describe how auditory localization is organized in the cortex. What is the evidence that A1 is important for localization?
8. What are the *what* and *where* auditory pathways? How are they related to the anterior and posterior belt areas?
9. What is the difference between listening to sound outdoors and indoors? Why does listening indoors create a problem for the auditory system?
10. What is the precedence effect, and what does it do for us perceptually?
11. What are some basic principles of architectural acoustics that have been developed to help design concert halls?
12. Describe some of the techniques used to manipulate the acoustics of some modern concert halls.

12.4 Auditory Scene Analysis

Our discussion so far has focused on localization—where a sound is coming from. We saw that the auditory system uses differences in level and timing between the two ears plus spectral information from sound reflections inside the pinnae to localize sounds. We now add an important complication that occurs constantly in the environment: multiple sources of sound.

At the beginning of the chapter, in Scenario 3, we described two people talking in a noisy coffee shop, with the sounds of music, other people talking, and the espresso machine in the background. The array of sound sources at different locations in the environment is called the **auditory scene**, and the process by which the stimuli produced by each source are separated is called **auditory scene analysis** (ASA) (Bregman, 1990, 1993; Darwin, 2010; Yost, 2001).

Auditory scene analysis poses a difficult problem because the sounds from different sources are combined into a single acoustic signal, so it is difficult to tell which part of the signal is created by which source just by looking at the waveform of the sound stimulus. We can better understand what we mean when we say that the sounds from different sources are combined into a single acoustic signal by considering the trio in **Figure 12.16**. The guitar, the vocalist, and the keyboard each create their own sound signal, but all of these signals enter the listener's ear together and so are combined into a single complex waveform. Each of the frequencies in this signal causes the basilar membrane to vibrate, but just as in the case of the bird and the cat in Figure 12.1, in which there was no information on the cochlea for the locations of the two sounds, it isn't obvious

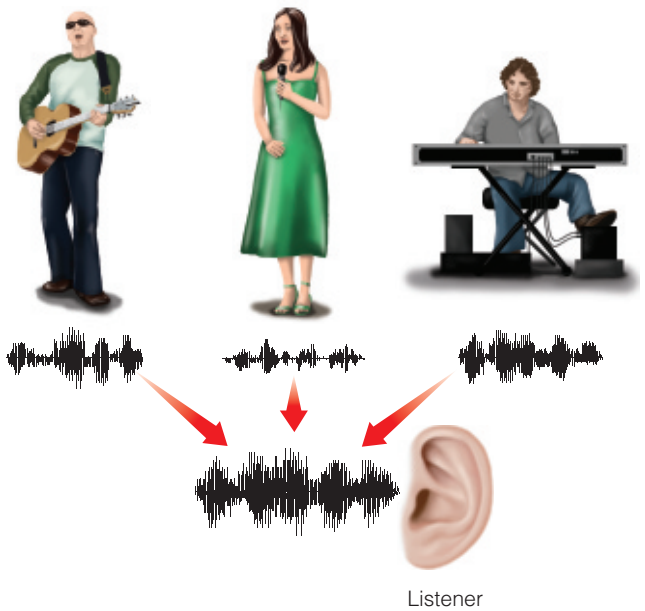

Figure 12.16 Each musician produces a sound stimulus, but these signals are combined into one signal, which enters the ear.

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what information might be contained in the sound signal to indicate which vibration is created by which sound source.

Auditory scene analysis, the process by which the auditory scene is separated into separate sources, considers two situations. The first situation involves **simultaneous grouping**. This occurs for our musical trio, because all of the musicians are playing simultaneously. The question asked in the case of simultaneous grouping is "How can we hear the vocalist and each of the instruments as separate sound sources?" Our example in Scenario 3, in which the many different sounds reach the listener's ears in the coffee shop are perceived as coming from separate sources, is another example of simultaneous grouping.

The second situation in ASA is **sequential grouping**—grouping that occurs as sounds follow one another in time. Hearing the melody being played by the keyboard as a sequence of notes that are grouped together is an example of sequential grouping, as is hearing the conversation of a person you are talking with in a coffee shop as a stream of words coming from a single source. Research on ASA has focused on determining cues or information in both of these situations.

Simultaneous Grouping

To begin our discussion of simultaneous grouping let's return to the problem facing the auditory system, when the guitar, keyboard, and vocalist create pressure changes in the air, and these pressure changes are combined to create a complex pattern of basilar membrane vibration.

How does the auditory system separate the frequencies in the "combined" sound signal into the different sounds made by the guitar, the vocalist, and the keyboard, when all are playing at the same time? In Chapter 5, we posed an analogous question for vision when we asked how elements in a scene become grouped together to create separate objects. One of the answers for vision is provided by the principles of perceptual organization proposed by the Gestalt psychologists and others, that is based on what usually occurs in the environment (see page 94).

A similar situation occurs for auditory stimuli, because a number of principles help us perceptually organize elements of an auditory scene, and these principles are based on how sounds are usually organized in the environment. We will now consider a number of different types of information that are used to analyze auditory scenes.

Location One way to analyze an auditory scene into its separate components would be to use information about where each source is located. According to this idea, you can separate the sound of the vocalist from the sound of the guitar based on localization cues such as the ILD and ITD. Thus, when two sounds are separated in space, the cue of location helps us separate them perceptually. In addition, when a source moves, it typically follows a continuous path rather than jumping erratically from one place to another. For example, this continuous movement of sound helps us perceive the sound from a passing car as originating from a single source.

But the fact that information other than location is also involved becomes obvious when we consider that sounds can be separated even if they are all coming from the same location. For example, we can perceive many different instruments in a composition that is recorded by a single microphone and played back over a single loudspeaker (Litovsky, 2012; Yost, 1997).

Onset Synchrony Onset time is one of the strongest cues for segregation. If two sounds start at slightly different times, it is likely that they came from different sources. This occurs often in the environment, because sounds from different sources rarely start at exactly the same time (Shamma & Micheyl, 2010; Shamma et al., 2011).

Timbre and Pitch Sounds that have the same timbre or pitch range are often produced by the same source. A flute, for example, doesn't suddenly sound like the timbre of a trombone. In fact, the flute and trombone are distinguished not only by their timbres, but also by their pitch ranges. The flute tends to play in a high pitch range, and the trombone in a low one. These distinctions help the listener decide which sounds originate from which source.

Harmonicity Remember from Chapter 11 that periodic sounds consist of a fundamental frequency, plus harmonics that are multiples of the fundamental (Figure 11.5). Because it is unlikely that several independent sound sources would create a fundamental and the pattern of harmonics associated with it, when we hear a harmonic series we infer that it came from a single source.

Sequential Grouping

The question of how we group sequences of sounds that occur over time also involves Gestalt grouping principles that influence how components of stimuli are grouped together (Chapter 5, page 96).

Similarity of Pitch We've mentioned, in discussing simultaneous grouping, how differences in the pitch of a flute and trombone help us isolate them as separate sources. Pitch also helps us organize the sound from a single source in time. Similarity comes into play because consecutive sounds produced by the same source usually are similar in pitch. That is, they don't usually jump wildly from one pitch to a very different pitch.

As we will see when we discuss music in Chapter 13, musical sequences typically contain small intervals between notes. These small intervals cause notes to be grouped together, following the Gestalt law of proximity (see page 98). The perception of a string of sounds as belonging together is called **auditory stream segregation** (Bregman, 1990; Michaeyl & Oxenham, 2010).

Albert Bregman and Jeffrey Campbell (1971) demonstrated auditory stream segregation based on pitch by alternating high

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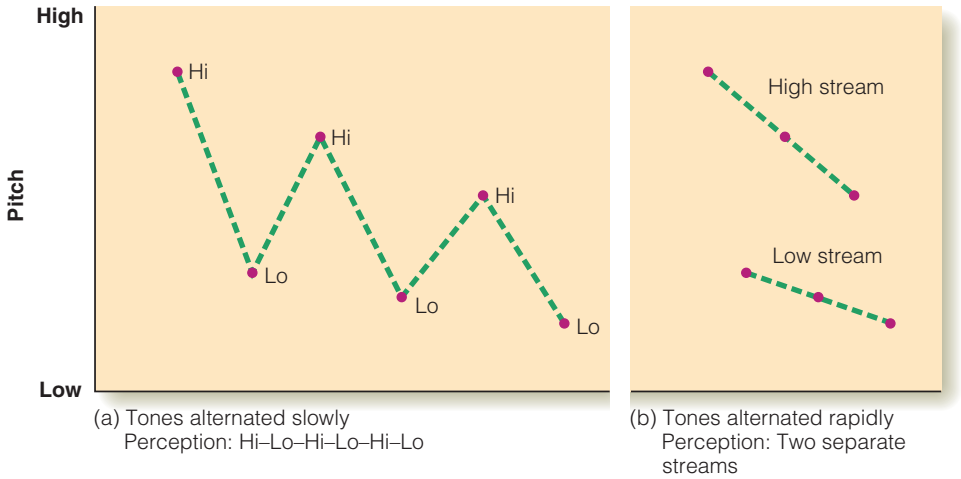

Figure 12.17 (a) When high and low tones are alternated slowly, auditory stream segregation does not occur, so the listener perceives alternating high and low tones. (b) Faster alternation results in segregation into high and low streams.

and low tones, as shown in the sequence in **Figure 12.17**. When the high-pitched tones were slowly alternated with the low-pitched tones, as in **Figure 12.17a**, the tones were heard as part of one stream, one after another: Hi–Lo–Hi–Lo–Hi–Lo, as indicated by the dashed line. But when the tones were alternated very rapidly, the high and low tones became perceptually grouped into two auditory streams; the listener perceived two separate streams of sound, one high-pitched and one low-pitched (**Figure 12.17b**) (see Heise & Miller, 1951, and Miller & Heise, 1950, for an early demonstration of auditory stream segregation). This demonstration shows that stream segregation depends not only on pitch but also on the rate at which tones are presented.

Figure 12.18 illustrates a demonstration of grouping by similarity of pitch in which two streams of sound are perceived as separated until their pitches become similar. One stream is a series of repeating notes (red), and the other is a scale that goes up (blue) (**Figure 12.18a**). **Figure 12.18b** shows how this stimulus is perceived if the tones are presented fairly rapidly.

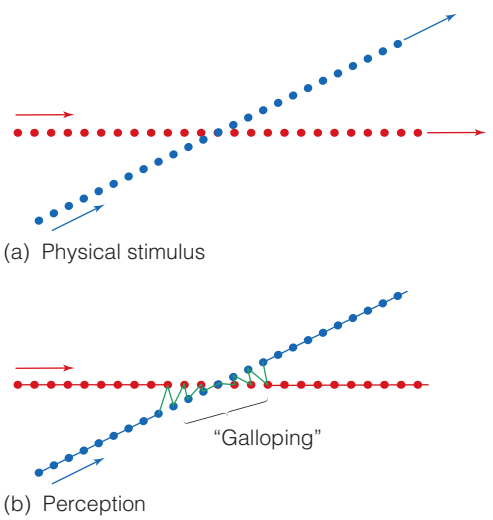

Figure 12.18 (a) Two sequences of stimuli: a sequence of similar notes (red), and a scale (blue). (b) Perception of these stimuli: Separate streams are perceived when they are far apart in frequency, but the tones appear to jump back and forth between stimuli when the frequencies are in the same range.

At first the two streams are separated, so listeners simultaneously perceive the same note repeating and a scale going up. However, when the frequencies of the two stimuli become similar, something interesting happens. Grouping by similarity of pitch occurs, and perception changes to a back-and-forth "galloping" between the tones of the two streams. Then, as the scale continues upward so the frequencies become more separated, the two sequences are again perceived as separated.

Another example of how similarity of pitch causes grouping is an effect called the **scale illusion**, or **melodic channeling**. Diana Deutsch (1975, 1996) demonstrated this effect by presenting two sequences of notes simultaneously through earphones, one to the right ear and one to the left (**Figure 12.19a**).

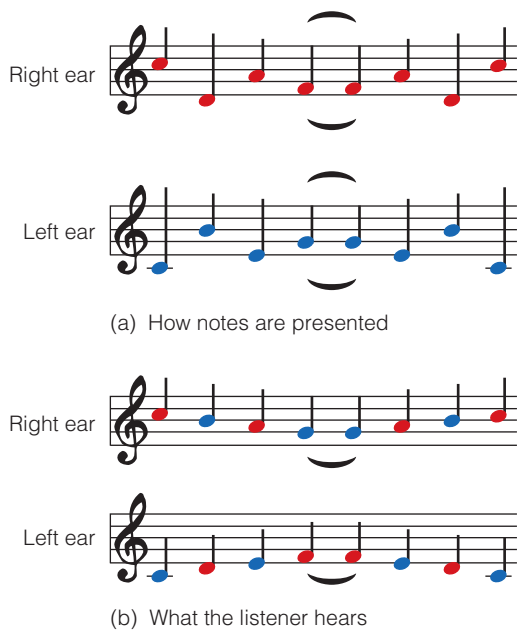

Figure 12.19 (a) These stimuli were presented to a listener's left ear (blue) and right ear (red) in Deutsch's (1975) scale illusion experiment. Notice how the notes presented to each ear jump up and down. (b) Although the notes in each ear jump up and down, the listener perceives a smooth sequence of notes. This effect is called the scale illusion, or melodic channeling. (From Deutsch, 1975)

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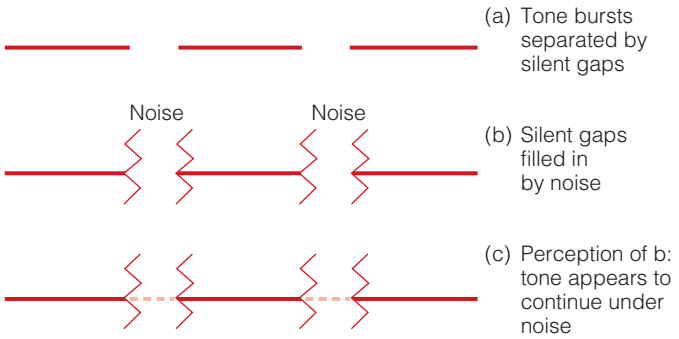
(a) Tone bursts separated by silent gaps
Noise
Noise
(b) Silent gaps filled in by noise
(c) Perception of b: tone appears to continue under noise

Figure 12.20 A demonstration of auditory continuity, using tones.

Notice that the notes presented to each ear jump up and down and do not create a scale. However, Deutsch's listeners perceived smooth sequences of notes in each ear, with the higher notes in the right ear and the lower ones in the left ear (**Figure 12.19b**). Even though each ear received both high and low notes, grouping by similarity of pitch caused listeners to group the higher notes in the right ear (which started with a high note) and the lower notes in the left ear (which started with a low note).

In Deutsch's experiment, the perceptual system applies the principle of grouping by similarity to the artificial stimuli presented through earphones and creates the illusion that smooth sequences of notes are being presented to each ear. However, most of the time, principles of auditory grouping like similarity of pitch help us to accurately interpret similar sounds as coming from the same source, because that is what usually happens in the environment.

Auditory Continuity Sounds that stay constant or that change smoothly are often produced by the same source. This property of sound leads to a principle that resembles the Gestalt principle of good continuation for vision (see Chapter 5, page 96). Sound stimuli with the same frequency or smoothly changing frequencies are perceived as continuous even when they are interrupted by another stimulus (Deutsch, 1999).

Richard Warren and coworkers (1972) demonstrated auditory continuity by presenting bursts of tone interrupted by gaps of silence (**Figure 12.20a**). Listeners perceived these tones as stopping during the silence. But when Warren filled in the gaps with noise (**Figure 12.20b**), listeners perceived the tone as continuing behind the noise (**Figure 12.20c**). This demonstration is analogous to the demonstration of visual good continuation illustrated by coiled rope in Figure 5.15 (see page 97). Just as the rope is perceived as continuous even when it is covered by another coil of the rope, a tone can be perceived as continuous even though it is interrupted by bursts of noise.

Experience The effect of past experience on the perceptual grouping of auditory stimuli can be demonstrated by presenting the melody of a familiar song, as in **Figure 12.21a**. These are the notes for the song "Three Blind Mice," but with the notes jumping from one octave to another. When people first hear these notes, they find it difficult to identify the song. But once they have heard the song as it was meant to be played (**Figure 12.21b**), they can follow the melody in the octave-jumping version shown in Figure 12.21a.

This is an example of the operation of a **melody schema**—a representation of a familiar melody that is stored in a person's memory. When people don't know that a melody is present, they have no access to the schema and therefore have nothing with which to compare the unknown melody. But when they know which melody is present, they compare what they hear to their stored schema and perceive the melody (Deutsch, 1999; Dowling & Harwood, 1986).

Each of the principles of auditory grouping that we have described provides information that helps us determine how sounds are grouped together across time. There are two important messages that we can take away from these principles. First, because the principles are based on our past experiences, and what usually happens in the environment, their operation is an example of prediction at work.

You may remember the statement "The brain is a prediction machine" from the Something to Consider section "Prediction Is Everywhere" at the end of Chapter 7. In that discussion we noted how prediction is involved in perceiving objects by making inferences about the image on the retina (Chapter 5); keeping a scene stationary as we move our eyes to scan the scene; anticipating where to direct our attention when making a peanut butter and jelly sandwich or driving down the street (Chapter 6); putting ketchup on that burger, and predicting other people's intentions (Chapter 7); and keeping a scene stationary as we follow a moving object with our eyes (Chapter 8).

Because prediction is so central to vision, it may be no surprise that it is also involved in hearing (and, yes, you were warned this was coming back in Chapter 7). Although we haven't specifically mentioned prediction in this chapter, we

Figure 12.21 "Three Blind Mice." (a) Jumping octave version. (b) Normal version.

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can appreciate that just as principles of visual organization provide information about what is *probably* happening in a visual scene, so the principles of auditory organization provide information about what is *probably* happening in an auditory scene. This leads to the second message, which is that each perceptual principle alone is not foolproof.

What this means is that basing our perceptions on just one principle can lead to error—as in the case of the scale illusion, which is purposely arranged so that similarity of pitch creates an erroneous perception. However, in most naturalistic situations, we base our perceptions on a number of these cues working together and predictions about what is "out there" become stronger when supported by multiple sources of evidence.

SOMETHING TO CONSIDER:

Interactions Between Hearing and Vision

The different senses rarely operate in isolation. We see people's lips move as we listen to them speak; our fingers feel the keys of a piano as we hear the music the fingers are creating; we hear a screeching sound and turn to see a car coming to a sudden stop. All of these combinations of hearing and other senses are examples of **multisensory interactions**. We will focus on interactions between hearing and vision.

One area of multisensory research is concerned with one sense "dominating" the other. If we ask whether vision or hearing is dominant, the answer is "it depends." As we will see next, in some cases vision dominates hearing.

The Ventriloquism Effect

The **ventriloquism effect**, or **visual capture**, is an example of vision dominating hearing. It occurs when sounds coming from one place (the ventriloquist's mouth) appear to come from another place (the dummy's mouth). Movement of the dummy's mouth "captures" the sound (Soto-Faraco et al., 2002, 2004).

Another example of visual capture occurred in movie theaters before the introduction of digital surround sound. An actor's dialogue was produced by a speaker located on one side of the screen but the image of the actor who was talking was located in the center of the screen, many feet away. Despite this separation, moviegoers heard the sound coming from its seen location (the image at the center of the screen) rather than from where it was actually produced (the speaker to the side of the screen). Sound originating from a location off to the side was captured by vision.

The Two-Flash Illusion

But vision doesn't always win out over hearing. Consider, for example, an amazing effect called the **two-flash illusion**. When a single dot is flashed onto a screen (**Figure 12.22a**), the participant perceives one flash. When a single beep is presented at the same time as the dot, the participant still perceives one flash. However, if the single dot is accompanied by two beeps, the participant sees two flashes, even though the dot was flashed only once (**Figure 12.22b**). The mechanism responsible for this effect is still being researched, but the important finding for our purposes is that sound creates a visual effect (de Haas et al., 2012).

Visual capture and the two-flash illusion, although both impressive examples of auditory–visual interaction, result in perceptions that don't match reality. But sound and vision occur together all the time in real-life situations, and when they do, they often complement each other, as when we are having a conversation.

Understanding Speech

When you are having a conversation with someone, you are not only hearing what the person is saying, but you may also

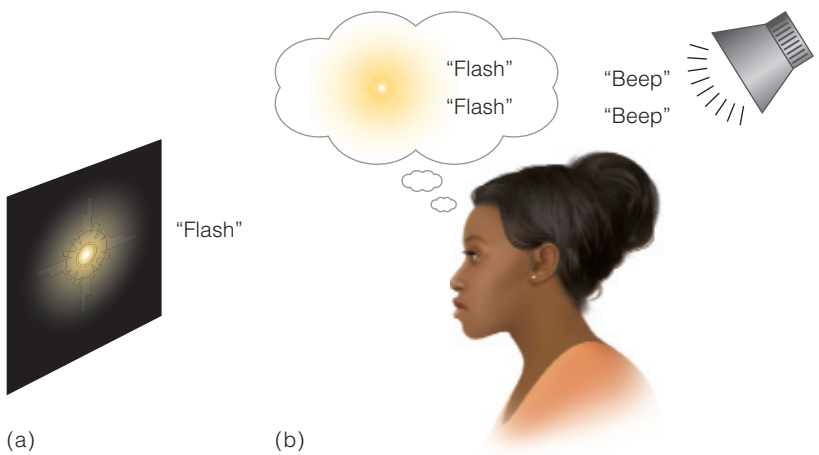

Figure 12.22 The two-flash illusion. (a) A single dot is flashed on the screen. (b) When the dot is flashed once but is accompanied by two beeps, the observer perceives two flashes.

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be watching his or her lips. Watching people's lip movements makes it easier to understand what they are saying, especially in a noisy environment. This is why theater lighting designers often go to great lengths to be sure that the actors' faces are illuminated. Lip movements, whether in everyday conversations or in the theater, provide information about what sounds are being produced. This is the principle behind **speechreading** (sometimes called lipreading), which enables deaf people to determine what people are saying by watching their lip and facial movements. In the chapter on speech perception, we will consider some additional examples of interactions between vision and speech.

Interactions in the Brain

The idea that there are connections between vision and hearing is also reflected in the interconnection of the different sensory areas of the brain (Murray & Spierer, 2011). These connections between sensory areas contribute to coordinated receptive fields (RFs) like the ones shown in **Figure 12.23** for a neuron in the monkey's parietal lobe that responds to both visual stimuli and sound (Bremmer, 2011; Schlack et al., 2005). This neuron responds when an auditory stimulus is presented in an area that is below eye level and to the left (**Figure 12.23a**) and when a visual stimulus originates from about the same area (**Figure 12.23b**). **Figure 12.23c** shows that there is a great deal of overlap between these two receptive fields.

It is easy to see that neurons such as this would be useful in our multisensory environment. When we hear a sound coming from a specific location in space and also see what is producing the sound—a musician playing or a person talking—the multisensory neurons that fire to both sound and vision help us form a single representation of space that involves both auditory and visual stimuli.

Another example of cross-talk in the brain occurs when the primary receiving area associated with one sense is activated by stimuli that are usually associated with another sense. An example is provided by some blind people who used a technique called *echolocation* to locate objects and perceive shapes in the environment.

Echolocation in Blind People

Daniel Kish, who has been blind since he was 13-months-old, finds his way around by clicking his tongue and listening to the echoes that bounce off of nearby objects. This technique, which is called **echolocation**, enables Kish to identify the location and size of objects while walking. **Figure 12.24** shows Kish hiking in Iceland. He uses tongue clicks to locate nearby objects using echolocation, and the canes to detect details of the terrain. (See Kish's TED talk "How I Use Sonar to Navigate the World" at www.ted.com.)

To study the effect of echolocation on the brain, Lore Thaler and coworkers (2011) had two expert echolocators create their clicking sounds as they stood near objects, and recorded the sounds and resulting echoes with small microphones placed in the ears. To determine how these sounds would activate the brain, they recorded brain activity using fMRI as the expert echolocators and sighted control participants listened to

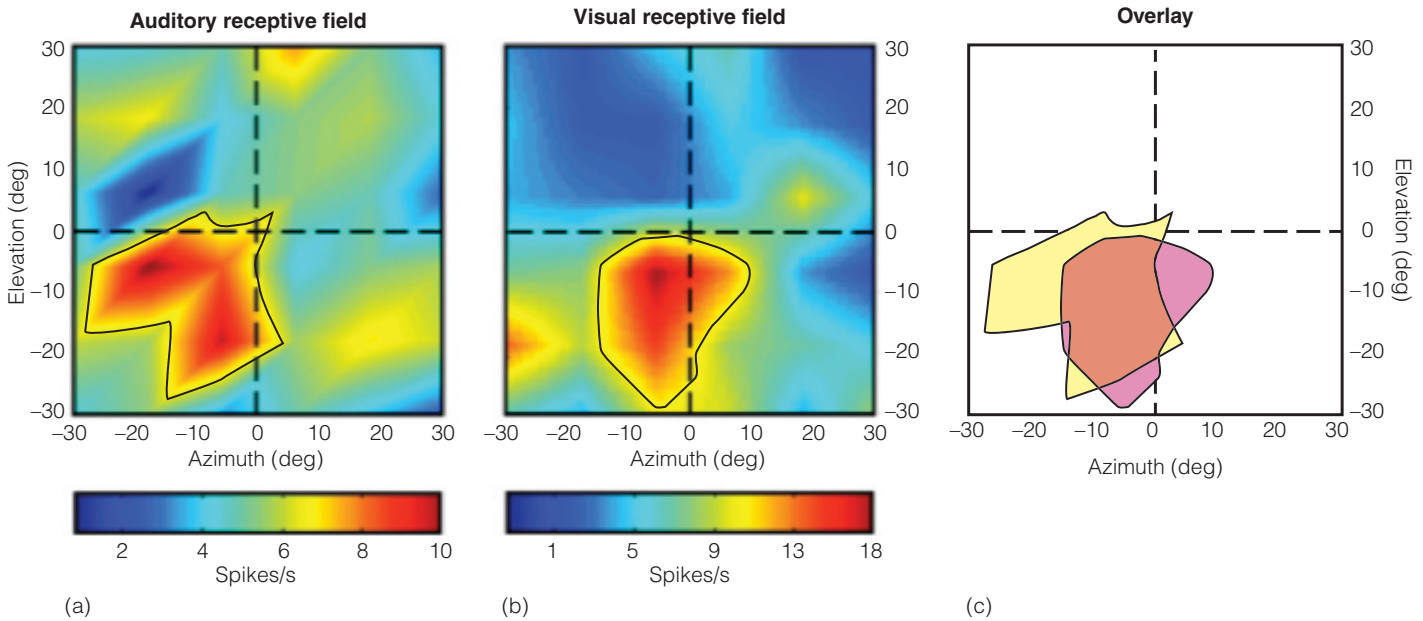

Figure 12.23 Receptive fields of neurons in the monkey's parietal lobe that respond to (a) auditory stimuli that are located in the lower left area of space and (b) visual stimuli presented in the lower left area of the monkey's visual field. (c) Superimposing the two receptive fields indicates that there is a high level of overlap between the auditory and visual fields. [(a) and (b) from Bremmer, 2011]

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Daniel Kish

Figure 12.24 Daniel Kish hiking in Iceland. Kish, who is blind, uses the canes to detect details of the terrain, and echolocation to locate nearby objects.

the recorded sounds and their echoes. Not surprisingly, they found that the sounds activated the auditory cortex in both the blind and sighted participants. However, the visual cortex was also strongly activated in the echolocators but was silent in the control participants.

Apparently, the visual area is activated because the echolocators are having what they describe as "spatial" experiences. In fact, some echolocators lose their awareness of the auditory clicks as they focus on the spatial information the echoes are providing (Kish, 2012). This report that echoes are transformed into spatial experiences inspired Liam Norman and Lore Thaler (2019) to use fMRI to measure the location of activity in expert echolocators' visual cortex as they listened to echoes coming from different locations. What they found was that echoes coming from a particular position in space tended to activate a particular area in the visual cortex. This link between the location of an echo and location on the visual cortex did not occur for control groups of blind non-echolocators and sighted participants.

What their result means, according to Norman and Thaler, is that learning to echolocate causes reorganization of the brain, and the visual area is involved because it normally contains a "retinotopic map" in which each point on the retina is associated with a specific location of activity in the visual cortex (see page 75). The maps for echolocation in the echolocator's visual cortex are therefore similar to the maps of visual locations in sighted people's visual cortex. Thus, when sound is used to achieve spatial awareness, the visual cortex becomes involved.

Listening to or Reading a Story

The idea that the brain's response can be based not on the type of energy entering the eyes or ears but on the outcome of the energy is also illustrated in an experiment by Mor Regev and coworkers (2013), who recorded the fMRI response of participants as they either listened to a 7-minute spoken story or read the words of the story presented at exactly the same rate that the words had been spoken. Not surprisingly, they found that listening to the story activated the auditory receiving area in the temporal lobe and that reading the written version activated the visual receiving area in the occipital lobe. But moving up to the superior temporal gyrus in the temporal lobe, which is involved in language processing, they found that the responses from listening and from reading were synchronized in time (**Figure 12.25**). This area of the brain is therefore responding not to "hearing" or "vision," but to the meaning of the messages created by hearing or vision. (The synchronized responding did not occur in a control group that was exposed to unidentifiable scrambled letters or sounds.) In the chapter on speech perception, we will venture further into the idea that sound can create meaning, and will describe additional relationships between sound and vision and sound and meaning.

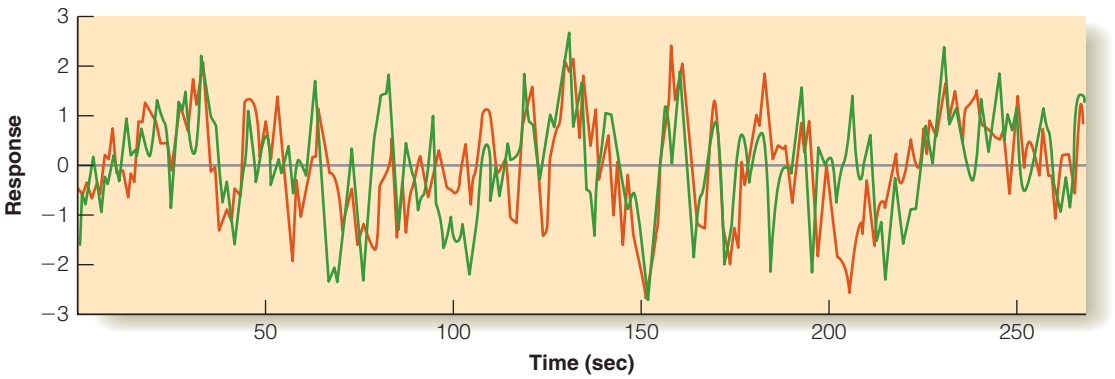

Figure 12.25 fMRI responses of the superior temporal gyrus, which is an area that processes language. Red: Response to *listening* to a spoken story. Green: Response to *reading* the story at exactly the same rate as it was spoken. The responses do not match exactly, but are highly correlated (correlation = 0.47). (From Regev et al., 2013)

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TEST YOURSELF 12.2

1. What is auditory scene analysis, and why is it a "problem" for the auditory system?
2. What is simultaneous grouping?
3. Describe the following types of information that help solve the simultaneous grouping problem: location, onset synchrony, timbre, pitch, and harmonicity.
4. What is sequential grouping?
5. Describe how the following are related to the sequential grouping problem: auditory stream segregation, the scale illusion, auditory continuity, and experience.
6. Describe why we can say that the principles of auditory scene analysis involve prediction.
7. Describe the ways that (a) vision dominates hearing and (b) hearing dominates vision.
8. Describe how visual and auditory receptive fields can overlap. What is the function of this overlap?
9. What is echolocation, as applied to blind people?
10. How does echolocation affect the brain?
11. Describe the experiment in which brain activity in the superior temporal gyrus in the temporal lobe was measured when listening to a story and when reading a story. What does the result of this experiment demonstrate about what this brain area is responding to?

THINK ABOUT IT

1. We can perceive space visually, as we saw in the chapter on depth perception, and through the sense of hearing, as we have described in this chapter. How are these two ways of perceiving space similar and different? (p. 292)
2. How good are the acoustics in your classrooms? Can you hear the professor clearly? Does it matter where you sit? Are you ever distracted by noises from inside or outside the room? (p. 299)
3. How is object recognition in vision like stream segregation in hearing? (p. 303)
4. What are some situations in which (a) you use one sense in isolation and (b) the combined use of two or more senses is necessary to accomplish a task? (p. 306)

KEY TERMS

Acoustic shadow (p. 293)
Anterior belt area (p. 299)
Architectural acoustics (p. 301)
Auditory localization (p. 292)
Auditory scene (p. 302)
Auditory scene analysis (p. 302)
Auditory space (p. 292)
Auditory stream segregation (p. 303)
Azimuth (p. 293)
Binaural cue (p. 293)
Coincidence detectors (p. 297)
Cone of confusion (p. 294)
Direct sound (p. 299)
Distance (p. 293)
Echolocation (p. 307)
Elevation (p. 293)
Indirect sound (p. 299)
Interaural level difference (ILD) (p. 293)
Interaural time difference (ITD) (p. 293)
ITD detector (p. 297)
ITD tuning curves (p. 297)
Jeffress model (p. 296)
Location cues (p. 293)
Melodic channeling (p. 304)
Melody schema (p. 305)
Multisensory interactions (p. 306)
Posterior belt area (p. 299)
Precedence effect (p. 300)
Reverberation time (p. 301)
Scale illusion (p. 304)
Sequential grouping (p. 303)
Simultaneous grouping (p. 303)
Spectral cue (p. 294)
Speechreading (p. 307)
Two-flash illusion (p. 306)
Ventriloquism effect (p. 306)
Visual capture (p. 306)
What auditory pathway (p. 299)
Where auditory pathway (p. 299)

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Music has been described as "a form of emotional communication" and as "organized sound." What's special about music is not only that it causes people to perceive rhythm and melody, but that it also causes them to experience emotions and memories, and sometimes even makes people feel like moving.

Nick White/Getty Images

Learning Objectives

After studying this chapter, you will be able to ...

- Answer the questions "What is music?" "Does music have an adaptive function?" and "What are the benefits of music?"
- Understand the different aspects of musical timing, including the beat, meter, rhythm, and syncopation.
- Describe how the mind can influence the perception of meter.
- Understand the different properties of melodies.
- Describe behavioral and physiological evidence that explains the connection between music and emotion.
- Understand the evidence for and against the idea that music and language share mechanisms in the brain.
- Describe experiments that have studied how infants respond to the beat.
- Understand what it means to say that music is "special."

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CHAPTER 13

Perceiving Music

CHAPTER CONTENTS

13.1 What Is Music?

13.2 Does Music Have an Adaptive Function?

13.3 Outcomes of Music
Musical Training Improves Performance in Other Areas
Music Elicits Positive Feelings
Music Evokes Memories

13.4 Musical Timing
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Syncopation
The Power of the Mind

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Trajectories
Tonality

TEST YOURSELF 13.1

13.6 Creating Emotions
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Expectancy and Emotion in Music

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SOMETHING TO CONSIDER: Comparing Music and Language Mechanisms in the Brain
Evidence for Shared Mechanisms
Evidence for Separate Mechanisms

DEVELOPMENTAL DIMENSION: How Infants Respond to the Beat
Newborns' Response to the Beat
Older Infants' Movement to the Beat
Infants' Response to Bouncing to the Beat

METHOD: Head-Turning Preference Procedure

13.7 Coda: Music Is "Special"

TEST YOURSELF 13.2

THINK ABOUT IT

Some Questions We Will Consider:

- What is music and what is its purpose? (p. 311)
- What aspects of music lead us to experience emotions? (p. 321)
- How can we compare the brain mechanisms of music and language? (p. 327)
- Can infants respond to the beat? (p. 329)

Music is a special type of sound. One thing that makes it special, which we noted in Chapter 11, is that musical pitches have a regularly repeating pattern of pressure changes, in contrast to the more random pressure changes of many environmental noises such as the sound of waves crashing. But what's really special about music is its popularity. While it is unlikely that someone would spend much time listening to individual tones, people spend vast amounts of time listening to sequences of tones strung together to create songs, melodies, or longer compositions. But, as we will see, music not only has melody, it also has rhythm, a beat that causes people to move, and music also elicits memories, feelings, and emotions.

13.1 What Is Music?

Most people know what music is, but how would you describe it to someone who has never heard it? One answer to this question might be the following definition provided by Leonard Meyer (1956), one of the early music researchers, who said that music is "a form of emotional conversation." Edgar Varèse, the French composer, defined music as "organized sound" (Levitin and Tirovolas, 2009). Wikipedia, borrowing from Varèse, defines music as "an art form and cultural activity whose medium is sound organized in time."

These definitions of music may make sense to someone who already knows what music is, but would likely leave a

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person unfamiliar with music in the dark. Perhaps more helpful is considering the following basic properties of music:

1. Pitch—The quality of tones that extends from "high" or "low," and that is often organized on a musical scale; the aspect of perception associated with musical melodies (**Figure 13.1a**) (See Chapter 11, page 270.)
2. Melody—A sequence of pitches that are perceived as belonging together (**Figure 13.1b**)
3. Temporal structure—The time dimension of music, which consists of a regular beat, organization of the beat into measures (meter), and the time pattern created by the notes (rhythm)
4. Timbre—The various qualities of sound that distinguish different musical instruments from one another
5. Harmony, consonance, dissonance—The qualities of sound (positive or negative) created when two or more pitches are played together

These properties describe how the various qualities of music sound. A song has a recognizable melody created by sequences of tones with different pitches. It has a rhythm, with some notes being longer than others, some more emphasized. Its timbre is determined by which instruments play it, or if it is sung by a male or a female. And its sound is affected by whether it is played as single notes or as a series of chords.

But there is more to music than properties like pitch, rhythm, and timbre. There are also people's responses to music, one of the most prominent being emotional. After all, Meyer's definition of music as "emotional conversation" identifies emotion as a central feature of music, and as we will see, a great deal of research has been done on the connection between music and emotion.

Other responses to music are movement, which occurs when we tap our feet or dance in response to music or play a musical instrument, and memory, when music creates new memories or brings back memories from our past. So music creates responses that affect many aspects of our lives. Perhaps this is what the 19th century philosopher Fredrich Nietzsche meant when he said, "without music life would be a mistake."

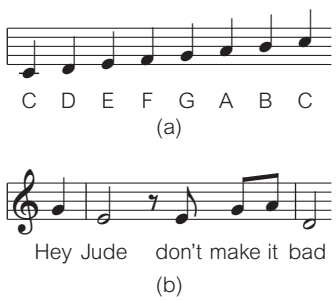

Figure 13.1 (a) A musical scale, in which notes are arranged in pitch from low to high. (b) A melody in which notes are perceived as belonging together. The melody's rhythm is determined by how the notes are arranged in time.

13.2 Does Music Have an Adaptive Function?

How would you answer the question: "What is the purpose of music?" One possible answer is that "its purpose is to help people have fun." Another is "to make people feel good." After all, music is pervasive in our environment—people listen to it all the time, both electronically and at concerts, and many people create it by singing or playing musical instruments.

A skeptic might respond to this answer by saying that it's fine that music is fun and people seek it out, but we need to ask larger questions of why music has become part of human life across all societies and what biological function it might have. Vision and hearing allow us to navigate in the environment safely and effectively, but what is the value of music? Asking this question involves asking whether music has had a purpose in evolution. That is, does music have an adaptive function that has enhanced humans' ability to survive?

An evolutionary adaptation is a function which evolved specifically to aid in survival and reproduction. Does music qualify? Charles Darwin's (1871) answer to this question was that humans sang before they spoke, and so music served the important purpose of laying the foundation for language. Additionally, Darwin saw music as being a way to attract sexual partners (Miller, 2000; Peretz, 2006). At the other extreme, Steven Pinker (1997) described music as "auditory cheesecake" arguing that music is constructed from mechanisms serving functions such as emotion and language.

Perhaps the strongest argument that music is an evolutionary adaptation is its role in social bonding and group cohesion, which facilitates people working together in groups (Koelsch, 2011). After all, only humans learn to play musical instruments and make music cooperatively in groups, and the ability to synchronize movements in a group to an external pulse is uniquely human and increases feelings of social bonding (Koelsch, 2018; Stupacher et al., 2017; Tarr et al., 2014; 2016).

The question of whether music has had an adaptive function is difficult to answer conclusively, because it involves making an inference about something that happened long ago (Fitch, 2015; Peretz, 2006). There is no question, however, of the importance of music to humans. Music has played an important role in human cultures throughout history; ancient musical instruments—flutes made of vulture bones—have been found that are 30,000–40,000 years old, and it is likely that music dates back to the human beginnings 100,000–200,000 years ago (Jackendoff, 2009; Koelsch, 2011). Music is also found in every known culture worldwide (Trehub et al., 2015). A recent analysis of music in 315 cultures concluded that although there are many differences in music in different cultures, there are similarities based on underlying psychological mechanisms (Mehr et al., 2019). Thus, although many different musical styles exist across cultures, ranging from Western classical music, to Indian Raga, to traditional Chinese music, to American jazz, the following characteristics of music are shared across cultures (Thompson et al., 2019).

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- Tones separated by octaves are perceived as similar.
- Music elicits emotions.
- Sequences of notes close in pitch are perceived as part of a group.
- Caregivers sing to their infants.
- Listeners move in synchrony with the music.
- Music is performed in social contexts.

13.3 Outcomes of Music

In addition to being universally prevalent and having important social functions, music has a number of positive outcomes. Here are three of them:

Musical Training Improves Performance in Other Areas

The effects of musical training are related to the fact that the brain is plastic—its neurons and connections can be shaped by experience (Reybrouck et al., 2018) (see Chapter 4, page 74). Musical training has been linked to better performance in mathematics, greater emotional sensitivity, improved language skills, and greater sensitivity to timing (Chobert et al., 2011; Krause and Chandrasekaran, 2010; Zatorre, 2013). In a study in which physicians and medical students were tested on their ability to detect heartbeat irregularities, it was found that doctors who played a musical instrument performed better than those without musical training (Mangione & Nieman, 1997).

Music Elicits Positive Feelings

Perhaps the most obvious benefit of music is that it makes us feel better. When people are asked why they listen to music, the two main reasons they cite are emotional impact and regulation of their emotions (Chanda & Levitin, 2013; Rentfro & Greenberg, 2019). It is not surprising, therefore, that the average person spends a great deal of time listening to music and considers it one of life's most enjoyable activities (Dube & La Bel, 2003). Not only does music make us feel better, but in some cases music results in feelings of transcendence and wonder or creates a pleasurable sensation of "chills" (Blood & Zatorre, 2001; Koelsch, 2014).

This link between music and feelings has caused music to be introduced in medical settings. Recently, for example, musicians have presented virtual concerts to both patients and health-care workers in COVID-19 hospital wards. One health-care worker's reaction to these concerts—"What can disrupt this pattern of despair is the music"—beautifully captures the healing power of music (Weiser, 2020).

Music Evokes Memories

Music has the power to elicit memories. If you've ever had a piece of music trigger a memory for something that you had experienced in the past, you have experienced a **music-evoked autobiographical memory (MEAM)**. MEAMs are often associated with strong emotions like happiness and nostalgia (Belfi et al., 2016; Janata et al., 2007), but can also be associated with sad emotions.

The ability of music to elicit memories has led to the use of music as a therapeutic tool for people with Alzheimer's disease, who typically suffer large impairments of memory. Mohamad El Haj and coworkers (2013) asked healthy control participants and participants with Alzheimer's to respond to the instruction "describe in detail an event in your life" after (1) two minutes of silence or (2) two minutes of listening to music that they had chosen. The healthy controls were able to describe autobiographical memories (memories about past life events) equally well in both conditions, but the memory of Alzheimer's patients was better after listening to the music (**Figure 13.2**).

The ability of music to elicit autobiographical memories in Alzheimer's patients inspired the film *Alive Inside* (Rossato-Bennett, 2014), which won the audience award at the 2014 Sundance Film Festival. This film documents the work of a nonprofit organization called Music & Memory (musicandmemory.org), which distributed iPods to hundreds of long-term care facilities for use by Alzheimer's patients. In a memorable scene, Henry, who suffers from severe dementia, is shown immobile and unresponsive to questions and what is going on around him (**Figure 13.3a**). But when the therapist puts earphones on Henry and turns on the music, he comes alive. He starts moving to the beat. He sings along with the music. And, most important of all, memories that had been locked away by Henry's dementia are released, and he becomes able to talk about some things he remembers from his past (**Figure 13.3b**). (Also see

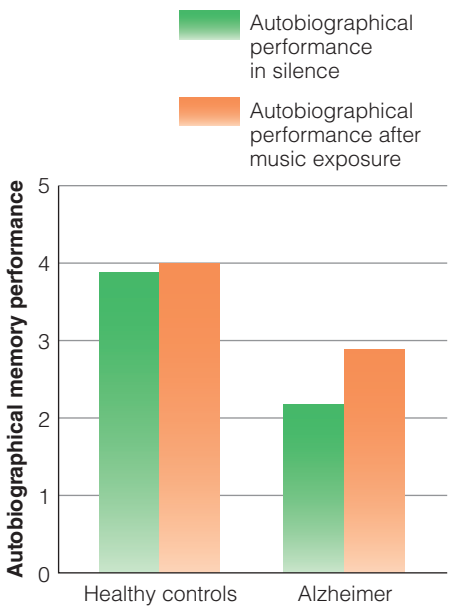

Figure 13.2 The results of El Haj et al.'s (2013) experiment, in which normal control participants (left pair of bars) had better autobiographical memory than Alzheimer's patients (right pair of bars). Alzheimer's patients' autobiographical memory was enhanced by listening to music that was meaningful to them. (Source: El Haj et al., 2013)

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Alive Inside LLC

Figure 13.3 Stills from the film *Alive Inside*. (a) Henry in his usual unresponsive state. (b) Henry listening and singing along with music that was meaningful to him. Listening to music also enhanced Henry's ability to talk with his caregivers.

Baird & Thompson, 2018, 2019; Heaton, 2009; and Kogutek et al., 2016 for more on the therapeutic effects of music.)

One reason for all these benefits is that music activates many areas across the brain. **Figure 13.4** illustrates the brain areas associated with musical activity (Levitin & Tirovolas, 2009). Daniel Levitin (2013) notes that "musical behaviors activate nearly every region of the brain that has so far been mapped." The figure identifies the auditory cortex as involved, because it is where sounds are initially processed. But many "non-auditory" areas are also activated by music, among them the amygdala and nucleus acumbus (creating emotions), the hippocampus (eliciting memories), the cerebellum and motor cortex (eliciting movement), the visual cortex (reading music, watching performances), sensory cortex (touch feedback from playing music), and the prefrontal cortex (creating expectations about what will happen next in a musical composition). Given music's wide reach across the brain, it is no wonder that its effects range from improving mood, to enhancing memory and moving in synchrony with other people. We begin describing how music works by describing two basic characteristics of music, timing and melody.

13.4 Musical Timing

We begin by describing the time dimension of music. We can distinguish a number of different properties that connect music and time.

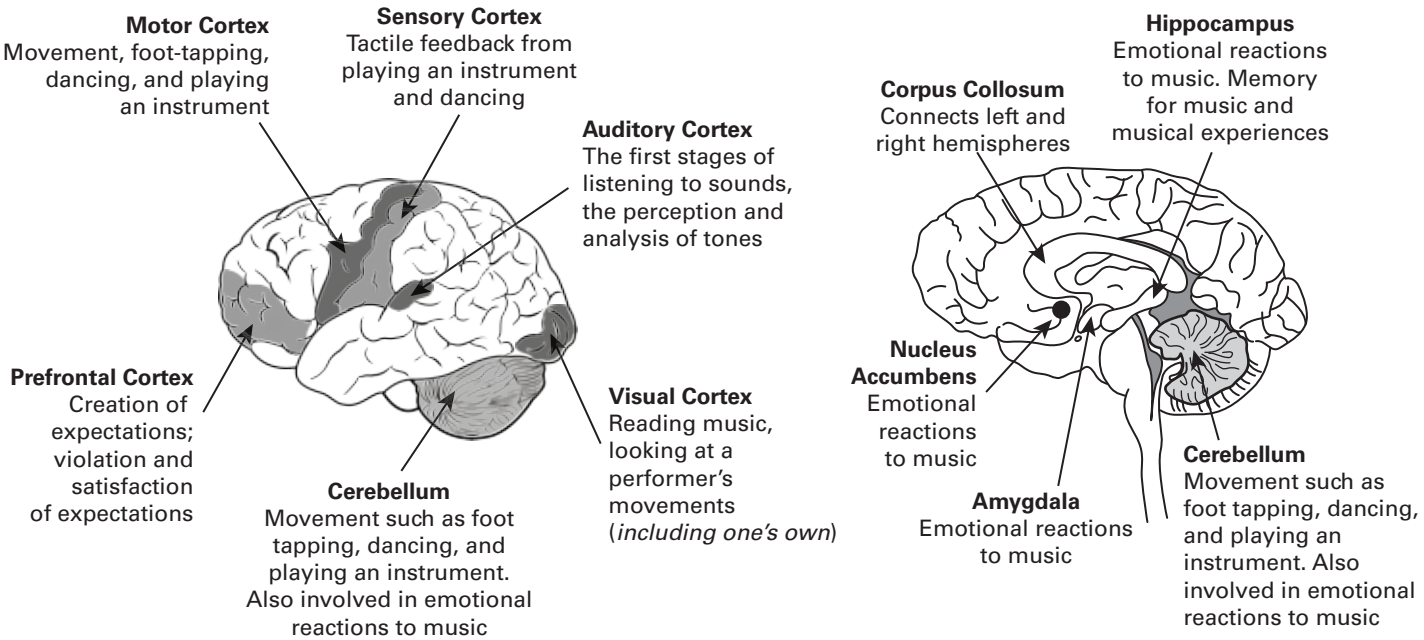
Motor Cortex
Movement, foot-tapping, dancing, and playing an instrument
Sensory Cortex
Tactile feedback from playing an instrument and dancing
Auditory Cortex
The first stages of listening to sounds, the perception and analysis of tones
Prefrontal Cortex
Creation of expectations; violation and satisfaction of expectations
Visual Cortex
Reading music, looking at a performer's movements (*including one's own*)
Cerebellum
Movement such as foot tapping, dancing, and playing an instrument. Also involved in emotional reactions to music
Hippocampus
Emotional reactions to music. Memory for music and musical experiences
Corpus Collosum
Connects left and right hemispheres
Nucleus Accumbens
Emotional reactions to music
Amygdala
Emotional reactions to music
Cerebellum
Movement such as foot tapping, dancing, and playing an instrument. Also involved in emotional reactions to music

Figure 13.4 Core brain regions associated with musical activity.

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The Beat

Every culture has some form of music with a **beat** (Patel, 2008). The beat can be up front and obvious, as in rock music, or more subtle, as in a quiet lullaby, but it is always there, sometimes operating alone, most of the time creating a framework for notes that create a rhythmic pattern and a melody. The beat is often accompanied by movement, as when musicians and listeners tap their toes while playing or listening, or when people get up and dance.

The link between the beat and movement is expressed not only by behaviors such as tapping or swinging in time to the beat, but also by responses of motor areas in the brain. Jessica Grahn and James Rowe (2009) demonstrated a connection between the beat and a group of subcortical structures at the base of the brain called the *basal ganglia*, which had been associated with movement in previous research. Their participants listened to "beat" patterns in which short notes falling on the beat created high awareness of the beat, and non-beat patterns in which longer notes created a weak awareness of the beat.

As participants listened, staying perfectly still in an fMRI brain scanner, their brain activity showed that the basal ganglia response was greater to the beat stimuli than to the non-beat stimuli. In addition, they determined that neural connectivity between subcortical structures and cortical motor areas, calculated by determining how well the response of one structure can be predicted from the response of a connected structure (see Figure 2.20) (Friston et al., 1997), was greater for the beat condition (**Figure 13.5**).

Another link between beat and movement was demonstrated by Joyce Chen and coworkers (2008) who measured activity in the premotor cortex in three conditions: (1) Tapping: Participants tapped along with the sequence. (2) Listening with anticipation: Participants listened to the sequence, but they knew they would be asked to tap to it later. (3) Passive listening: Participants listened passively to a rhythmic sequence. It isn't surprising that tapping caused the greatest response, because the premotor cortex is involved in creating movements. But a response also occurred in the listening with anticipation condition (70 percent of the response to tapping) and in the passive listening condition (55 percent of the response to tapping), even though participants were just listening, without moving. Thus, just as Grahn and Rowe found that just listening to beat stimuli activated the basal ganglia, Chen and coworkers found that motor areas in the cortex are activated just by listening to a beat, which, Chen suggests, may partially explain the irresistible urge to tap to the beat when hearing music.

Taking this auditory-motor connection a step farther, Takako Fujioka and coworkers (2012) measured people's brain waves as they listened to sequences of beats at different tempos. Their results, in **Figure 13.6**, show that the brain waves oscillate in time with the beat. The peak of the wave occurs on the beat, the wave then decreases and rebounds to predict the next beat. Underlying this response are neurons that are tuned to specific time intervals (see also Schaefer et al., 2014).

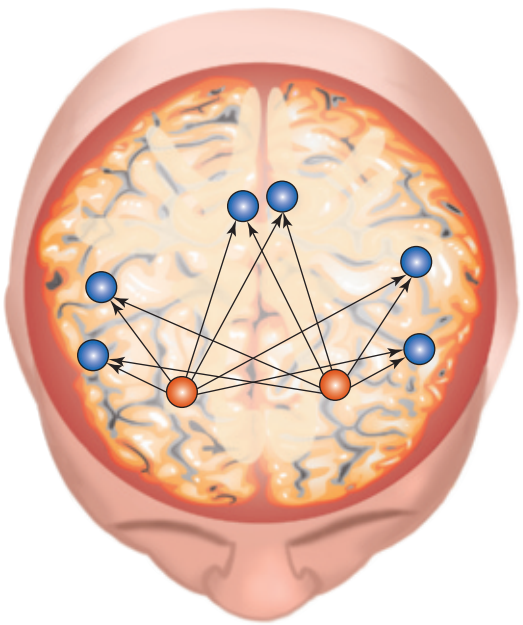

Figure 13.5 Grahn and Rowe (2009) found that connectivity between subcortical structures (red) and cortical motor areas (blue) was increased for the beat condition compared to the non-beat condition.

Meter

Meter is the organization of beats into bars or measures, with the first beat in each bar often being accented (Lerdahl & Jackendorff, 1983; Plack, 2014; Tan et al., 2013). There are two

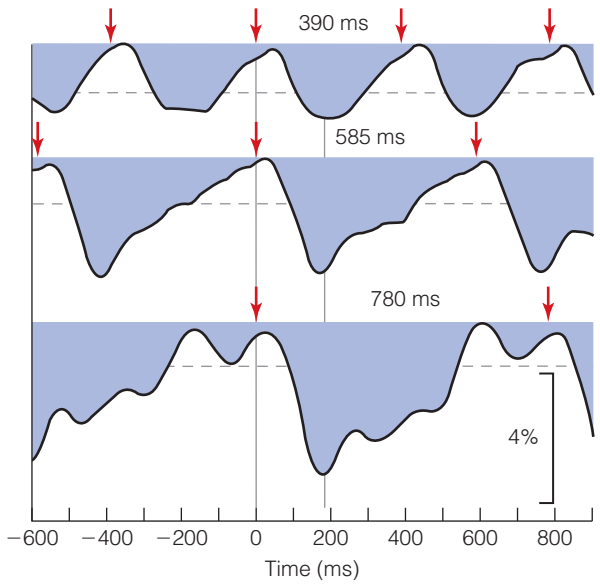

Figure 13.6 Time course of brain activity measured on the surface of the skull in response to sequences of equally spaced beats, indicated by the arrows. Numbers indicate spacing, in milliseconds, between each beat. The fastest tempo (about 152 beats per minute) is at the top, and the slowest (about 77 beats per minute) is on the bottom. The brain oscillations match the beats, peaking just after the beat, decreasing, and then rebounding to predict the next beat. (Fujioka et al., 2012)

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basic kinds of meter in Western music: **duple meter** in which accents are in multiples of two, such as 12 12 12 or 1234 1234 1234, like a march; and **triple meter**, in which accents are in groups of three, such as 123 123 123, as in a waltz.

Metrical structure can be achieved if musicians accentuate some notes by using a stronger attack or by playing them louder or longer. In the most common metric structure, called 4:4 time, the first of every four beats is accented, and is most easily understood by counting along, as in **1**-2-3-4-**1**-2-3-4. Focusing on these accented notes creates a kind of skeleton of the temporal flow of the music, where accented notes form the beats.

By accenting certain beats, musicians bring an expressiveness to music beyond what is heard by simply playing a string of notes. Thus, although the musical score may be the starting point for a performance, the musicians' *interpretation* of the score is what listeners hear, and the interpretation of which notes are accented can influence the perceived meter of the composition (Ashley, 2002; Palmer, 1997; Sloboda, 2000).

Rhythm

Music *structures* time by creating **rhythm**—the time pattern of durations created by notes (Tan et al., 2013; Thompson, 2015). Although we defined rhythm as the time pattern of durations, what is important is not the durations of *notes*, but the **inter-onset interval**—the time between the *onset* of each note. This is illustrated in **Figure 13.7**, which shows the first measures of "The Star Spangled Banner." Note onsets are indicated by the blue dots above the music, and the spaces between these dots define the song's rhythm. Because note *onsets* are what defines the rhythm, it is possible that two versions of this song, one in which the notes are played briefly with spaces in between (like notes plucked on a guitar) and another in which the notes are held so the spaces are filled (like a note bowed on a violin), can both have the same rhythm.

But whatever the rhythm, we always come back to the pulse of music—the beat—indicated by the red arrows in Figure 13.7. Although the beat is associated with specific notes in this example, the beat marks equally spaced pulses in time, and so occurs even when there are no notes (Grahn, 2009).

So the picture we have described is music as movement through time, propelled by beats that are organized by meter, which forms a framework for rhythmic patterns created by notes. One thing that this temporal flow creates is prediction. We know that a particular composition is going to be propelled along by the regularity of the beat, and—here's the important thing—this isn't simply an intellectual concept: the beat is a property that is transformed into behaviors like tapping the feat, swaying, and dancing.

The fact that the temporal components of music—the beat, rhythm, and meter—often elicit movement is important. But we have left out one important thing: we noted that the beat marks equally spaced pulses of time, so it occurs even when there are no notes. We now add to that the observation that sometimes notes occur off the beat, a phenomenon called *syncopation*.

Syncopation

Look back at the music for the Star Spangled Banner (Figure 13.7), and notice that each beat falls on the beginning of a note. Another example of the beat happening at the beginnings of notes is shown in **Figures 13.8a** (all quarter notes) and **13.8b** (the quarter notes are represented by joined eighth-notes). The match between meter and notes is obvious, with

Figure 13.8 Syncopation explained. (a) The top record shows a simple melody consisting of four quarter notes in the first measure. (b) The same melody, with each quarter note changed to two joined eighth notes. The count below this record indicates that each quarter note begins on the beat. This passage is therefore not syncopated. (c) Syncopation is created by adding an eighth note at the beginning. The count indicates that the three quarter-notes start off the beat (on "and"). This is an example of syncopation.

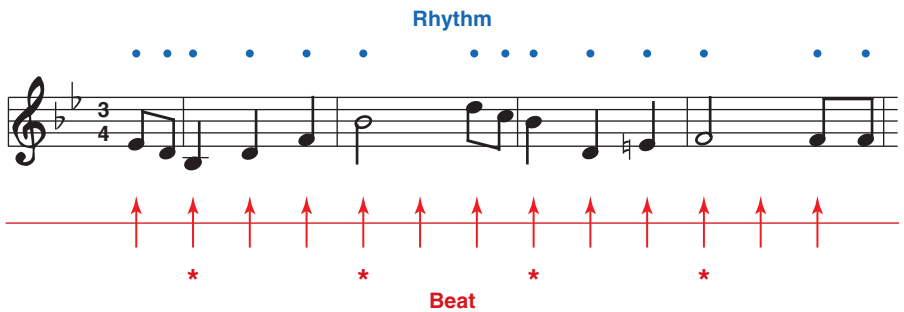

Figure 13.7 First line of "The Star-Spangled Banner." The blue dots indicate note onsets, which define the rhythm. The red arrows indicate the beat. The stars (*) indicate accented beats, which define the meter.

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the beat falling right at each beginning of each quarter note, as we count 1-and, 2-and, 3-and, 4-and.

But **Figure 13.8c** shows a situation in which this synchronized relation between the beat and the notes is violated. In this example, the eighth note added at the beginning changes the relation between the beat and the notes, so that the beat comes in the middle of each of the quarter-notes. These notes begin "off the beat" on the "and" count, which causes a "jumpiness" to the passage called syncopation.

Syncopated rhythms are at the heart of jazz and pop music. For example, consider **Figure 13.9**, the music to the Beatle's *Let It Be*. As in Figure 13.8c, some of the notes begin before the beat. The beginnings of the notes for the words *self* and *Mary*, indicated by the dashed arrows at (a) and (b), precede the beat, indicated by the red arrows. This slight mismatch between the beat and some notes has been linked to people's urge to dance, to "be in the groove" (Janata et al., 2011; Levitin et al., 2018).

Figure 13.10 shows that the brain's response to a less predictable syncopated series is larger than to a more predictable non-syncopated series (Vuust et al., 2009). As we will see when we discuss emotions, this larger brain response to syncopation is related to a difference between what a listener expects will happen in the music, and what actually happens.

The Power of the Mind

We've seen that meter is the organization of beats into measures, with the first beat in a bar often being accented. Although this seems to imply that meter is determined solely by the time signature of a musical composition, it turns out that meter is a cognitive function that can be created by the listener's mind (Honig & Bower, 2019).

Mind Over Meter How can metrical structure be created by the mind? Even though the ticking of a metronome creates a series of identical beats with regular spacing, it is possible to transform this series of beats into perceptual groups. We can, for example, imagine the beats of a metronome in duple meter

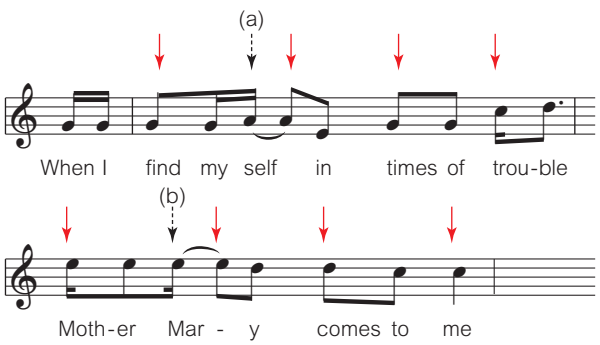

Figure 13.9 The Beatle's *Let It Be* contains syncopation. The beat is indicated by the red arrows. The dashed arrow at (a) shows that the beginning of the word *self* precedes the beat. Similarly, at (b) *Mary* begins before the beat.

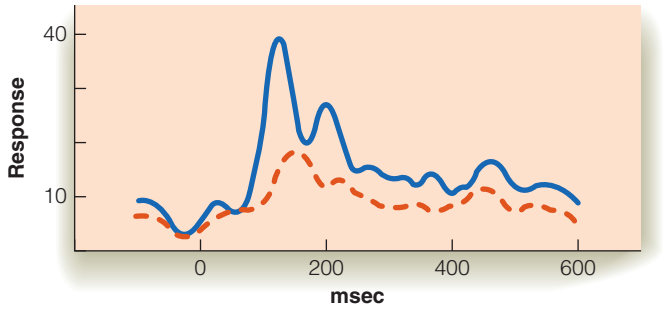

Figure 13.10 Brain response to non-syncopated melody (dashed line) and syncopated melody (solid line).

(TICK-toc) or, with a small amount of effort, in triple meter (TICK-toc-toc) (Nozaradan et al., 2011).

John Iversen and coworkers (2009) studied the mental creation of meter using magnetoencephalography (MEG) to measure participants' brain responses as they listened to rhythmic sequences. MEG measures brain responses by recording magnetic fields caused by brain activity and it records brain responses very rapidly, so responses to specific notes in a rhythmic pattern can be determined.

Participants listened to two-tone sequences and were told to mentally imagine that the beat occurred either on the first note or on the second note of each sequence. **Figure 13.11** shows that the MEG response depended on which beat was accented in the listener's mind with imagining the beat on the first note creating the blue curve and imagining the beat on the second note creating the red curve. Thus, our ability to change meter with our mind is reflected directly by activity in the brain.

Movement Influences Meter A song's meter, like the one-two-three of a waltz, influences how a dancer moves. But the relationship between music and movement can also occur in the opposite direction, because movement can influence the perceptual grouping or metrical structure of the beats. This was illustrated in an experiment in which the experimenter held hands with a participant as they bounced up and down in a duple pattern (every other beat) or a triple pattern (every third beat) (Phillips-Silver and Trainor, 2007). After bouncing with the experimenter, participants listened to duple and triple patterns and indicated which pattern they had heard while

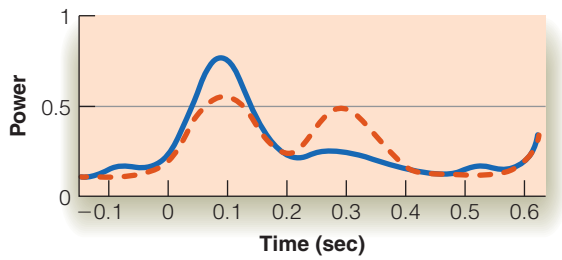

Figure 13.11 Results of the Iversen and coworkers (2009) experiment. Blue: MEG response when imagining the accent on the first note. Red: MEG response when imagining the accent on the second note.

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bouncing. On 86 percent of the trials, participants picked the pattern that matched the way they were bounced. This result also occurred when the participants were bounced while blindfolded, but not when they just watched the experimenter bounce.

Based on the results of these and other experiments, Phillips-Silver and Trainor concluded that the crucial factor that causes movement to influence the perception of metrical structure is stimulation of the **vestibular system**—the system that is responsible for balance and sensing the position of the body. To check this idea, Trainor and coworkers (2009) had adults listen to the ambiguous series of beats while electrically stimulating their vestibular system in a duple or triple pattern with electrodes placed behind the ear. This caused the listener to feel as if his or her head were moving back and forth, even though it remained stationary. This experiment duplicated the results of the other experiments, with listeners reporting hearing the pattern that matched the metrical grouping created by stimulating the vestibular system on 78 percent of the trials.

Language Stress Patterns Influence How Listeners Perceive Meter Perception of meter is influenced not only by movement but by longer-term experience—the stress patterns of a person's language. Different languages have different stress patterns, because of the way the languages are constructed. For example, in English, function words like "the," "a," and "to" typically precede content words, as in "the *dog*" or "to *eat*," where *dog* and *eat* are stressed when spoken. In contrast, Japanese speakers place function words after the content words, so "the *book*" in English (with *book* stressed) becomes "*hon ga*" in Japanese (with *hon* stressed). Therefore, the dominant stress pattern in English is *short–long* (*unaccented–accented*), but in Japanese it is *long–short* (*accented–unaccented*).

Comparisons of how native English-speakers and Japanese-speakers perceive metrical grouping supports the idea that the stress patterns in a person's language can influence the person's perception of grouping. John Iversen and Aniruddh Patel (2008) had participants listen to a sequence of alternating long and short tones (**Figure 13.12a**) and then indicate whether they perceived the tones' grouping as long–short or short–long. The results indicated that English-speakers were more likely to perceive the grouping as short–long (**Figure 13.12b**) and Japanese speakers were more likely to perceive the grouping as long–short (**Figure 13.12c**).

This result also occurs when comparing 7- to 8-month-old English and Japanese infants, but it does not occur for 5- to 6-month-old infants (Yoshida et al., 2010). It has been hypothesized that the shift that occurs between about 6 and 8 months happens because that is when infants are beginning to develop the capacity for language.

To end this section, let's consider two musical quotes. The first, "The beat goes on," is the title and first line of a song written by Sonny Bono in 1966. This idea is consistent with our description of how the beat, which pushes music through time, is an essential component of music. The beat of music has also been likened to our heartbeat, because just as our heartbeat keeps us alive, the musical beat is essential for music.

This brings us to our second quote, this one by Carlos Santana, which connects music and the heart in another way: "There's a melody in everything. And once you feel the melody, then you connect immediately with the heart... sometimes... language gets in the way. But nothing penetrates the heart faster than the melody." So we now turn to the melody.

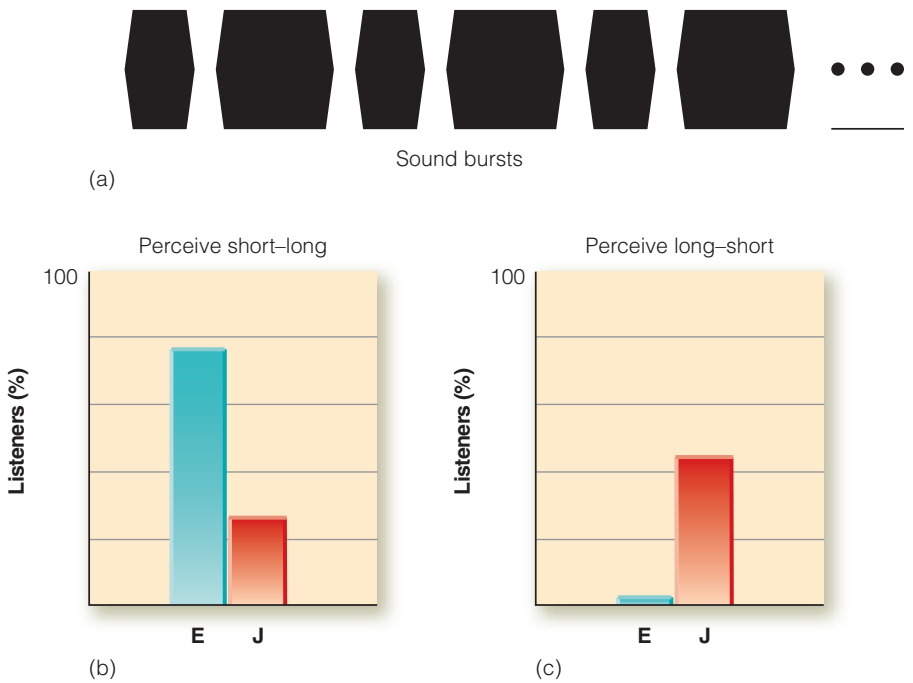

Figure 13.12 Differences between Japanese and American perceptions of meter. (a) Participants listened to sequences of short and long tones. On half the trials, the first tone was short; on the other half, long. The durations of the tones ranged from about 150 ms to 500 ms (durations varied for different experimental conditions), and the entire sequence repeated for 5 seconds. (b) English-speaking participants (E) were more likely than Japanese-speaking participants (J) to perceive the stimulus as short–long. (c) Japanese-speaking subjects were more likely than English-speaking subjects to perceive the stimulus as long–short. (Based on data from Iversen & Patel, 2008)

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13.5 Hearing Melodies

Now that we've considered the timing mechanisms that not only drive music through time, but influence how some parts of a composition are accentuated, we focus our attention on the notes. We've seen that notes create rhythm, which depends on the arrangement and duration of notes, and also that notes can be arranged in a way that creates the phenomenon of syncopation, which can lead to "the groove." But we now focus on how notes create melodies, because as Mozart declared, "melody is the essence of music."

We will be considering the following characteristics of melodies: (1) how notes are organized to create melodies; (2) how we perceive individual notes; and (3) how we are constantly predicting what notes are going to come next.

Organized Notes

Melody is defined as *the experience of a sequence of pitches as belonging together* (Tan et al., 2010), so when you think of the way notes follow one after another in a song or musical composition, you are thinking about its melody. Remember from Chapter 11 that one definition of pitch was *that aspect of auditory sensation whose variation is associated with musical melodies* (Plack, 2014), and it was noted that when a melody is played using frequencies above 5,000 Hz (where 4,166 Hz is the highest note on the piano), you can tell something is changing, but it doesn't sound musical. So melodies are more than just sequence of notes—they are sequences of notes that belong together and sound musical.

Also, remembering our discussion of auditory stream segregation in Chapter 12, we described some of the properties that create sequential grouping—similarity of pitch, continuity, and experience. These principles operate not only for music but also for other sounds including, notably, speech.

As we continue this discussion of grouping from Chapter 12, we are still interested in what causes notes to be grouped together, but as we focus on music, let's take a different approach. Assume you are a composer, and your goal is to create a melody. One way to approach this problem is to consider how other composers have arranged notes. We begin with intervals.

Intervals

One characteristic that favors grouping notes in Western music is the **interval** between notes. Small intervals are common in musical sequences, in accordance with the Gestalt principle of proximity we described in Chapter 5 (p. 98), which states that elements near each other tend to be perceived as grouped together (Bharacha & Krumhansl, 1983; Divenyi & Hirsh, 1978). Large intervals occur less frequently because large jumps increase the chances that the melodic line will break into separate melodies (Plack, 2014). The prevalence of small intervals is confirmed by the results of a survey of a large number of compositions from different cultures, which shows that the predominant interval is 1–2 **semitones**, where a semitone is the smallest interval used in Western music, roughly the distance between two notes in a musical scale, such as between C and C#, with 12 semitones in an octave (**Figure 13.13**) (Vos & Troost, 1989).

You can check the predominance of small intervals yourself by listening to music while paying attention to the spacing between successive pitches. Generally, you will find that most of the intervals are small. But there are exceptions. Consider, for example, the first two notes of "Somewhere Over the Rainbow" (*Some – Where*), which are separated by an octave (12 semitones), so they are perceptually similar. Generally, after a large jump, the melody turns around to fill in the gap, a phenomenon called **gap fill** (Meyer, 1956; Von Hipple & Huron, 2000).

Another way to describe how pitches become perceived as belonging together is to consider **musical phrases**—how notes are perceived as forming segments like phrases in language (Deutsch, 2013a; Sloboda & Gregory, 1980). To begin considering phrases, try imagining one of your favorite compositions (or, better yet, actually listen to one). As you hear one note following another, can you divide the melody into segments? A common way of subdividing melodies is into short segments called musical phrases, which are similar to phrases in language

Consider, for example, the first line of the song in **Figure 13.14**: *Twinkle, twinkle little star, how I wonder what you are*. We can split this sentence into two phrases separated by the comma between *star* and *how*. But if we didn't know the words and just listened to the music, it is likely that we would divide the melody into the same two phrases. When people are asked to listen to melodies and indicate the end of one unit and the beginning of the next, they are able to segment the melodies into phrases (Deliege, 1987; Deutsch, 2013a).

The most powerful cue for the perception of phrase boundaries is pauses, with longer intervals separating one phrase from another (Deutsch, 2013a; Frankland & Cohen, 2004). Another cue for phrase perception is the pitch intervals between notes. The interval separating the end of one phrase and the start of another is often larger than the interval separating two notes within a phrase.

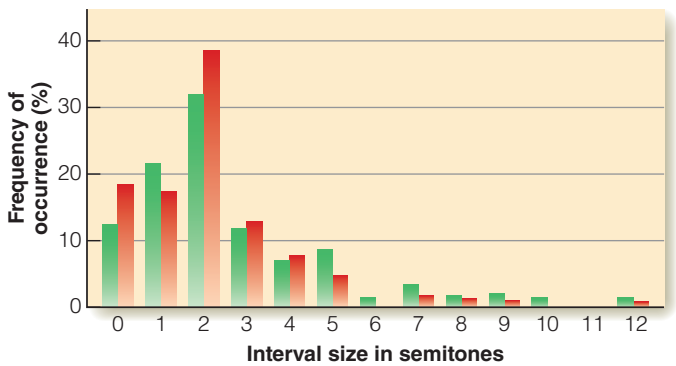

Figure 13.13 Frequency at which intervals occur in a survey of many musical compositions. Green bars: classical composers and the Beatles. Red bars: ethnic music from a number of different cultures. The most common interval is 1–2 semitones. (From Vos & Troost, 1989)

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Figure 13.14 The first line of "Twinkle, Twinkle, Little Star."

When David Huron (2006) measured intervals, in semitones, between the notes in 4,600 folk songs containing about 200,000 intervals, he found that the average interval within phrases was 2.0 semitones, whereas the average interval between the end of one phrase and the beginning of the next was 2.9 semitones. There is also evidence that longer notes tend to occur at the end of a phrase (Clark & Krumhansl, 1990; Deliege, 1987; Frankland & Cohen, 2004).

Trajectories

Certain *trajectories* of notes are commonly found in music. The **arch trajectory**—rise and then fall—is common (see the beginning of "Twinkle, Twinkle, Little Star" in Figure 13.14 for an example of this trajectory). Although there are fewer large changes in pitch than small changes, when large changes do occur, they tend to go up (as in the first two notes of "Somewhere Over the Rainbow"), and small changes are likely to descend (Huron, 2006).

Tonality

Another thing that determines how notes follow one another is tonality. **Tonality** refers to the way the various tones in music seem to vary between highly stable and highly unstable, as well as the way they help orient listeners as to what notes to expect next while a piece of music is playing. The most stable note within any key is called the **tonic**, which is the note that names the key, and we usually expect a melody to begin and end on the tonic note. This effect, which is called **return to the tonic**, occurs in "Twinkle, Twinkle, Little Star," which begins and ends on a C.

Each key is also associated with a scale. In Western music, the most common scale is the major scale, and consists of seven distinct notes, made famous in the song "Doh a Deer" (doh, re, me, fa, sol, la, ti, doh). The various notes in the scale vary in how stable they are perceived to be and how often we expect them to occur. We can specify a **tonal hierarchy** to indicate how stable each note is and so how well it fits within a scale. The tonic note has the greatest stability, the fifth note has the second highest level of stability, and the third note is next in stability. Thus for a scale in the key of C, which is associated with the scale C D E F G A B C, the three most stable notes would be C, G, and E, which together form the three-note C-major chord. Notes that are not in the scale have very low stability, and hence seldom occur in conventional Western music.

A classic experiment on tonality is one by Carol Krumhansl and Edward Kessler (1982), in which they measured perceptions of tonality by presenting a scale that established a major or minor key, and then following the scale with a probe tone. Listeners assigned a rating of 1–7 to the probe to indicate how well it fit with the scale presented previously (where 7 is the best fit). The results of this experiment, indicated by the red line in **Figure 13.15**, show that the tonic, C, received the highest rating, followed by G and E, which are notes 1, 5, and 3 of the C major scale. (Note that the experiment included keys in addition to C; this graph combines the results from all of the keys.) Other notes in the scale, D, F, A, B, received the next highest ratings, and notes not in the scale, like C# and F#, received the lowest ratings. Krumhansl's experiment therefore measured the tonal hierarchy for many different scales.

Krumhansl (1985) then considered the possibility that there is a relationship between the tonal hierarchy and the way notes are used in a melody by referring to statistical analyses of the frequency or duration of notes in compositions by composers such as Mozart, Schubert, and Mendelssohn (Hughes, 1977; Knopoff & Hutchinson, 1983; Youngblood, 1958). When she compared these analyses to her tonal hierarchy, she found an average correlation of 0.89. What this match means, says Krumhansl, is that listeners and composers have internalized the statistical properties of music and base their "best fit" ratings on the frequency with which they have heard these tonalities in compositions.

Krumhansl and Kessler's experiment required listeners to rate how well tones fit into a scale. The idea that certain notes are more likely to follow one another in a composition has also been demonstrated by the **cloze probability task**, in

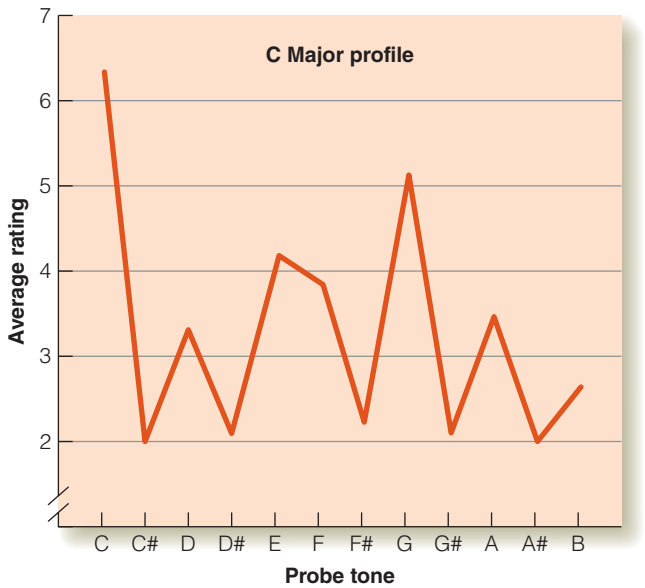

Figure 13.15 Ratings of Krumhansl and Kessler's (1982) probe tone experiment. Ratings indicate how well probe tones fit a scale, with 7 being the best possible fit. See text for details.

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Table 13.1 Commonly Occurring Properties of Phrases and Melodies

GROUPING	COMMON CHARACTERISTICS
Phrases	• Large time intervals between end of one phrase and beginning of the next • Large pitch intervals between phrases, compared to within phrases
Melody	• Melodies contain mostly small pitch intervals • Large pitch changes tend to go up • Smaller pitch changes are likely to go down • Downward pitch change often follows a large upward change • Melodies contain mostly tones that fit the melody's tonality • There is a tendency to return to the tonic at the end of a section of melody

which a listener is presented with a melody, which suddenly stops. The listener's task is to sing the note they think comes next. An experiment using this technique showed that listeners completed a novel melody by singing the tonic note on an average of 81 percent of the trials, with this number being higher for listeners with formal musical training (Fogel et al., 2015). Thus, as we listen to music, we are focusing on the notes we are hearing, while simultaneously anticipating the upcoming notes. This anticipation, which is a good example of prediction, affects grouping, with notes we anticipate being more easily grouped with other notes to create melody.

Table 13.1 summarizes a number of characteristics that are associated with musical grouping. These properties are not absolute—that is, they don't always occur in every melody. However, taken together they describe things that occur often in music, and thus are similar to the idea of *regularities in the environment*, which we introduced in our discussion of perceiving visual scenes in Chapter 5 (see page 105) and auditory prediction, which we discussed in Chapter 12 (see page 305). Just as knowledge from a lifetime of experience in viewing the environment can influence our perception of scenes and objects in visual scenes, a similar situation may occur for music, as listeners use their knowledge of regularities like the ones in Table 13.1 to predict what is going to happen next in a musical composition.

TEST YOURSELF 13.1

1. How has music been defined?
2. Describe five basic properties of music.
3. What is the purpose of music? Is music an evolutionary adaptation? What characteristics of music are shared across cultures?
4. Describe three benefits of music that are associated with performance, feelings, and memories.
5. Describe the beat. What is its purpose in music and what responses does it generate behaviorally and in the brain?
6. How are the results of Merchant's "oscillatory brain wave experiment" relevant to prediction?
7. What is meter? Metrical structure?
8. What is rhythm? How is it related to notes?
9. What is syncopation and what are its effects?
10. How is meter influenced by (a) the mind, (b) movement, and (c) patterns of a person's language?
11. What is melody?
12. What is the evidence that small intervals are associated with grouping that creates melody?
13. How are trajectories related to melodies?
14. Describe tonality, the tonic, return to the tonic, and tonal hierarchy.
15. Describe the cloze probability task. How was it used to demonstrate anticipation in music?
16. What is the relation between regularities in the environment and music, and a listener's ability to anticipate what is going to happen next in a musical composition?

13.6 Creating Emotions

We have been placing the elements of music under an analytical microscope, which has revealed things about how the timing and arrangement of pitches create the organized sounds of music. This approach is consistent with Varese's description of music from the beginning of the chapter as "organized sound." But to take in the full scope of music, we need to consider effects that extend beyond perception. We need to focus on Meyer's description of music as being "emotional communication."

Why are we interested in emotions in a book about perception? Because emotion is what gives music its power, and is a central reason that making and listening to music has occurred in every culture throughout human history. Ignoring emotion would, therefore, be ignoring an essential component of music, which is why emotion has been studied side-by-side with music perception.

Two approaches have been used by researchers to describe the emotional response to music: (1) the **cognitivist approach**, which proposes that listeners can perceive the emotional meaning of a piece of music, but that they don't actually feel the emotions, and (2) the **emotivist approach**, which proposes that a listener's emotional response to music involves actually feeling the emotions (Thompson, 2015).

One way to get in touch with these two approaches is to consider how music can affect people's experience when viewing a film. Imagine a tracking shot following two people walking down the street holding hands. It's a nice day, and they seem happy. But as they continue walking, a sound-track fades in. The music is slow and has a pulse to it that sounds rather foreboding, and you think "Something bad is about to happen to these people." In this case the music may be perceived as a cue of an upcoming threat, but it may not actually cause emotions in the viewer.

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Alternatively, there are situations in which intense music can cause viewers to feel emotions. An example is the shower scene in Alfred Hitchcock's *Psycho*, in which Norman Bates, played by Anthony Perkins, stabs Janet Leigh multiple times in the shower, accompanied by shrieking strings, and then a series of slow deep chords as the dying Janet Leigh slowly slides down the shower wall. For some people this music may just add some tension to the scene, but others may feel strong emotions that would not have occurred if the scene had been shot without a sound track. (Interestingly, Hitchcock had planned to show the shower scene without a sound track. Luckily for the film, Bernard Herrmann, the film's music director, convinced Hitchcock to add the music.)

Evidence for the emotivist approach has been provided by laboratory experiments in which participants are asked to indicate what they are feeling in response to different musical selections. Avram Goldstein (1980) asked participants to indicate when they experienced "thrills" as they listened to music through earphones, where thrills is defined by the Oxford English Dictionary as "a nervous emotion or tremor caused by intense emotional excitement... producing a slight shudder of tightening through the body." The results showed that many participants reported thrills that corresponded to the emotional peaks and valleys of the music. In another study, John Sloboda (1991) found that when musicians were asked to report their physical responses to music, the most common responses were shivers, laughter, lump in the throat, and tears.

Our concern here is how music causes emotions, either perceived or felt. If we were to ask this question about other aspects of life, such as reactions to life experiences or reading literature, the answer might be that emotions are often elicited by events or stories: A personal relationship begins or ends, a pet dies, you get a good grade on an exam. These kinds of events often elicit emotions. But there is a difference between event- or story-elicited emotions and music-elicited emotions. As Keith Oatley and Phillip Johnson-Laird (2014) point out with regard to literary fiction: "Stories can evoke real emotions about unreal events. You can laugh or weep about what you know are fictions. Music is more puzzling, because it can move you, even if it refers to nothing." So what is it about the sounds of music that can evoke strong emotions, even while referring to nothing?

Structural Features Linking Music and Emotion

When we discussed melody, we saw how various characteristics of music help create melodies (see Table 13.1). Researchers have taken the same approach to emotion by looking for connections between features of music and emotions. Thomas Eerola and coworkers (2013) had participants listen to musical compositions that varied along a number of dimensions, such as key: major or minor; tempo: slow to fast; register: ranging from lower pitched to higher pitched. The participants rated each selection on four dimensions: scary, sad, happy, and peaceful. **Figure 13.16** shows the results for the dimensions that had the largest effect on emotion: key and tempo. Major keys were associated with happy and peaceful; minor with scary and sad (**Figure 13.16a**); slow tempo

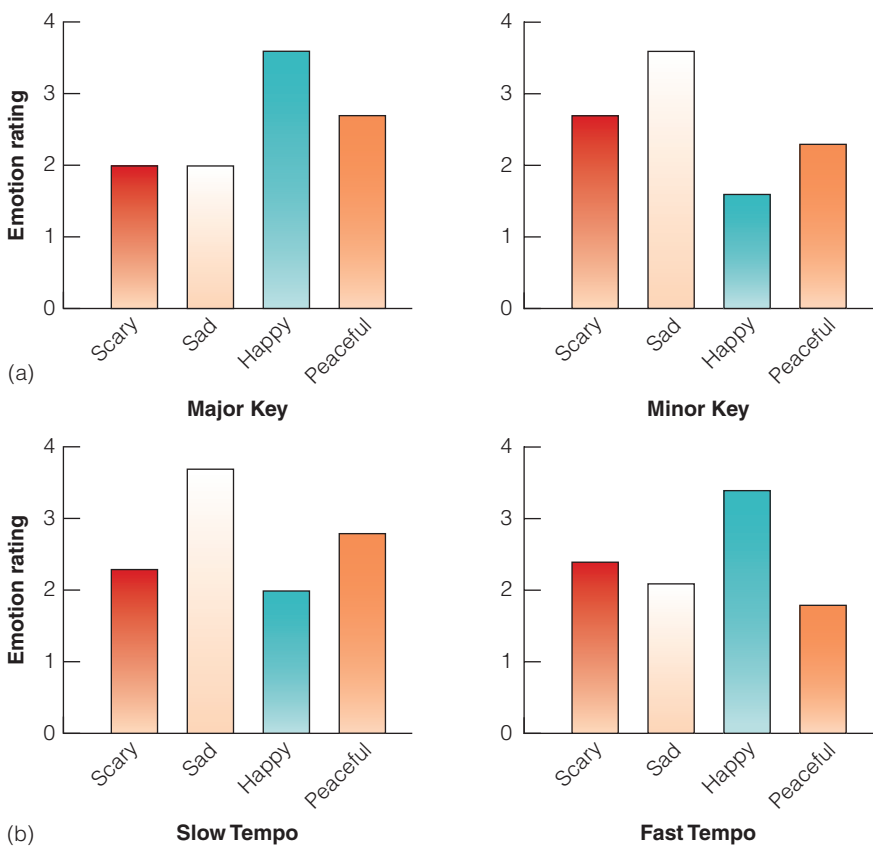

Figure 13.16 Emotional responses scary, sad, happy, and peaceful, that are associated with structural features of music. (a) Major and minor keys. Major keys are associated with happy and peaceful, whereas minor keys are associated with scary and sad. (b) Slow and fast tempos. Slow tempo is associated with sad and peaceful, whereas fast tempos are associated with happy. (Erola et al., 2013)

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with sad and peaceful; fast with happy (**Figure 13.16b**). Other dimensions also had effects: Increasing loudness caused an increase in scary and a decrease in peaceful. Increasing the register, so compositions were played with a higher pitch, caused a decrease in scary and an increase in happy.

One of the classic examples of a combination of a minor key, slow tempo and low register eliciting sadness, is Samuel Barber's *Adagio for Strings*, which won a 2004 British Broadcasting Company poll to identify "the saddest music in the world" by a wide margin (Larson, 2010). Barber's *Adagio* accompanies a scene at the end of the 1986 Vietnam-war film *Platoon*, in which battle-weary soldiers are slowly trudging across a field. The gravity of the scene combined with the effect of the music creates an almost unbearable feeling of sadness.

Other musical dimensions related to emotion have also been identified. For example, increasing dissonance (which occurs when combinations of notes don't sound harmonious when played together) causes an increase in tension (Koelsch, 2014). Loud music creates arousal, which is the brain's way of putting us on alert (Thompson, 2015). All of these results link specific properties of musical sounds to specific emotions.

Expectancy and Emotion in Music

Expectation is the feeling that we know what's coming up in music and is therefore another example of prediction. The beat creates a temporal expectation that says, "this is going to continue, with one beat following the other, so you know when to tap" (Zatorre et al., 2007). But what if the beat suddenly changes, as when a persistent drum-beat stops? Or if the relation between the beat and the notes becomes less predictable, as occurs in syncopation? As we saw in Figure 13.10, a less-predictable syncopated rhythm causes a larger response in the brain than a more predictable rhythm. Some results of a change in music that violates a person's expectations are surprise, tension, and emotion, and capturing the listener's attention.

Another example of expectation is when a musical theme is repeated over and over. For example, the famous beginning of Beethoven's Fifth Symphony (Da Da Da Daaah) is followed by many repetitions of that theme, which listeners anticipate throughout the first movement of the symphony. As Stefan Koelsch and coworkers (2019) state, "When listening to music, we constantly generate plausible hypotheses about what will happen next."

Expectation can also occur at a less conscious level, which is necessary because music, like language, often speeds by, leaving little time for conscious reflection (Ockelford, 2008). This happens in language, when we anticipate what words are most likely to come next in a sentence, and in music, as demonstrated by the cloze probability task (p. 320), when we anticipate which notes will come next (Fogel et al., 2015; Koelsch, 2011).

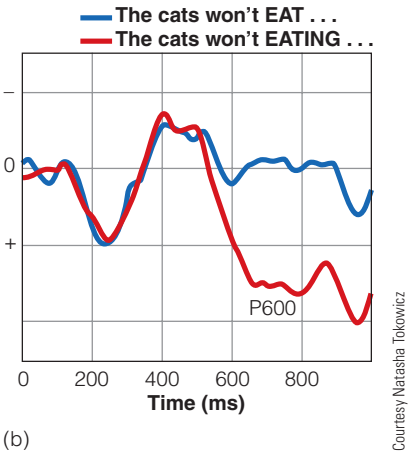
The idea that we have an expectancy, so we are constantly predicting what's coming next, raises a question similar to the one we asked about an unpredictable beat. What happens when expectations are violated so we expect one phrase or note but hear something else? The answer is that violations of expectancy for tones cause both physiological and behavioral effects (Huron, 2006; Meyers, 1956).

Research on expectancy for tones is based on the idea of **musical syntax**—"rules" that specify how notes and chords should be combined in music. The term **syntax** is associated more with language than with music. Syntax in language refers to grammatical rules that specify correct sentence construction. For example, the sentence "The cats won't eat" follows the rules of syntax, whereas the phrase "The cats won't eating" doesn't follow the rules. We will consider the idea of musical syntax shortly, but first we describe a way syntax has been studied in language using an electrical response called the *event-related potential*.

METHOD | Studying Syntax in Language Using the Event-Related Potential

The **event-related potential (ERP)** is recorded with small disc electrodes placed on a person's scalp, as shown in **Figure 13.17a**. Each electrode picks up signals from groups of neurons that fire together. A characteristic of the ERP that makes it useful for studying language (or music) is that it is

(a)



(b)

Courtesy Natasha Tokowicz

Figure 13.17 (a) A person wearing electrodes for recording the event-related potential (ERP). (b) ERP responses to *eat* (blue curve), which is grammatically correct, and *eating* (red curve), which is not grammatically correct, and so creates a P600 response. Note that positive is down in this record. ([b] From Osterhout et al. 1997)

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a rapid response, occurring on a time scale of fractions of a second, as shown in the responses of **Figure 13.17b**. The ERP consists of a number of waves that occur at different delays after a stimulus is presented. The one we are concerned with is called the P600 response, where *P* stands for "positive" and 600 indicates that it occurs about 600 milliseconds after the stimulus is presented. We are interested in the P600 response because it responds to violations of syntax (Kim & Osterhout, 2005; Osterhout et al., 1997). The two curves in Figure 13.17b illustrate this. The blue curve is the response that occurs after the word *eat* in the sentence "The cats won't eat." The response to this grammatically correct word shows no P600 response. However, the red curve, to the word *eating*, which is grammatically incorrect in the sentence "The cats won't eating," has a large P600 response. This is the brain's way of signaling a violation of syntax.

The reason for introducing the idea that the P600 response indicates violations of syntax in language is that the ERP has been used in a similar way to determine how the brain responds to violations of syntax in music. Aniruddh Patel and coworkers (1998) used this violation of musical syntax to see if the P600 response occurred in music. Their listeners heard a musical phrase like the one in **Figure 13.18a**, which contained a target chord, indicated by the arrow above the music. There were three different targets: (1) an "In key" chord that fit the piece, shown on the musical staff; (2) a "Nearby key" chord that

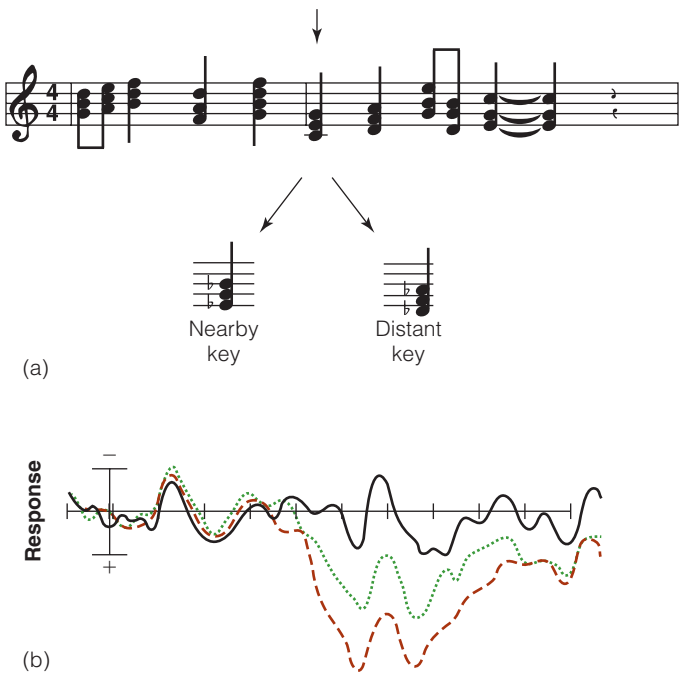

Figure 13.18 (a) The musical phrase heard by subjects in Patel and coworkers' (1998) experiment. The location of the target chord is indicated by the downward pointing arrow. The chord in the music staff is the "In key" chord. The other two chords were inserted in that position for the "Nearby key" and "Distant key" conditions. (b) ERP responses to the target chord: black = in key; green = nearby key; red = far key.

didn't fit as well; and (3) a "Distant key" chord that fit even less well. In the first part of the experiment, listeners judged the phrase as acceptable 80 percent of the time when it contained the in-key chord; 49 percent when it contained the nearby-key chord; and 28 percent when it contained the distant-key chord. Listeners were apparently judging how "grammatically correct" each version was.

Patel then used the event-related potential (ERP) to determine how the brain responds to these violations of syntax. **Figure 13.18b** shows that there is no P600 response when the phrase contained the in-key chord (black record), but that there are P600 responses for the two other chords, with the bigger response for the more out-of-key chord (red record). Patel concluded from this result that music, like language, has a syntax that influences how we react to it. Other studies following Patel's have confirmed that electrical responses like P600 occur to violations of musical syntax (Koelsch, 2005; Koelsch et al., 2000; Maess et al., 2001; Vuust et al., 2009).

Violating syntax generates a "surprise response" in the brain so when things get interesting or different, the brain perks up. This is interesting, but what do unfulfilled expectations that lead to surprise have to do with emotion in music? We can answer this question by considering what happens when the music fails to return the tonic (see page 320), because compositions often return to the tonic and listeners expect this to happen. But what if it doesn't? Try singing the first line of "Twinkle, Twinkle, Little Star," but stop at "you," before the song has returned to the tonic. The effect of pausing just before the end of the phrase, which could be called a violation of musical syntax, is unsettling and has us longing for the final note that will bring us back to the tonic.

The idea of a link between expectation and the emotional response to music has been the basis of proposals that composers can choose to purposely violate a listener's expectations in order to create emotion, tension, or a dramatic effect. Leonard Meyer suggested this in his book *Emotion and Meaning in Music* (1956), in which he argued that the principal emotional component of music is created by the composer's choreographing of expectation (also see Huron, 2006; Huron & Margulis, 2010). And just as music that meets the listener's expectations has its charms, music that violates expectation can create add to the emotional impact of music (Margulis, 2014). For example, Mozart used novelty to grab the listener's attention.

Figure 13.19 shows excerpts from Mozart's 31st Symphony. The top phrase, from the opening of the symphony, is an example of a composition that matches the listener's prediction, because the first notes are Ds, followed by a rapidly rising scale ending in D. This ending is highly expected, so listeners familiar with Western music would predict the D if the scale were to stop just before it was to happen. But something different happens in the bottom phrase, which occurs later in the symphony. In this phrase, the first notes are As, which, like the other phrase, are followed by a rapidly rising scale. But at the end of the scale, when listeners expect an A, they instead hear a B-flat, which doesn't sound like it fits the note predicted by the return to the tonic (Koelsch et al., 2019). This lack of fit

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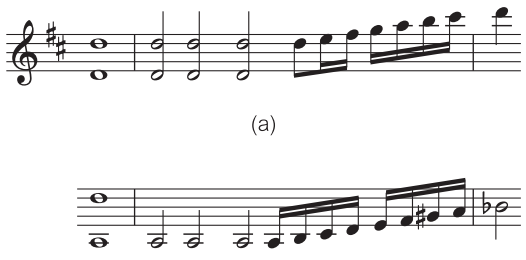

(a)

(b)

Figure 13.19 Passages from Mozart's Symphony No. 31. The final note in the top passage is expected, because it continues the scale leading up to it. The final note in the bottom passage is unexpected, because it doesn't continue the scale leading up to it.

is not, however, a mistake. It is Mozart's way of saying to the listener, "Listen up. Something interesting is happening!"

Physiological Mechanisms of Musical Emotions

The link between musical emotions and physiological responding has been studied in a number of ways, including recording electrical responses, brain scanning to identify the structures that are involved, brain scanning to identify chemical processes, and neuropsychological studies on the effect of brain damage on musical emotions.

Recording Electrical Responses We described Patel's (1998) experiment, which showed that the brain generates a P600 response to violations of musical syntax. Many experiments following Patel's have recorded similar responses to unexpected notes. For example, the unexpected note in Mozart's symphony generates a response called the **early right anterior negativity (ERAN)**, which occurs in the right hemisphere, slightly earlier than the P600 response recorded by Patel (Koelsch et al., 2019). Both of these electrical "surprise responses" are physiological signals linked to the surprise experienced by listeners.

Brain Scanning Another way to understand the physiology of emotion in music is to look at which structures are associated with musical emotions. We've seen that music activates areas throughout the brain (Figure 13.4), and the same story emerges when we consider the array of structures associated with the emotional processing of music. Brain imaging studies have identified a number of structures associated with music-associated emotions (Peretz, 2006). **Figure 13.20** shows the locations of three of these areas, the amygdala, which is also associated with the processing of non-musical emotions, the nucleus accumbens, which is associated with pleasurable experiences, including musical "chills," which often involve shaking and goosebumps, and the hippocampus, which is one of the central structures for the processing and storage of memories (Koelsch, 2014; Mori & Iwanaga, 2017).

In an early brain imaging study, Anne Blood and Robert Zatorre (2001) asked participants to pick a musical selection that consistently elicited pleasant emotional responses, including chills. These selections caused an increase in heart rate and brain waves compared to control music that didn't cause chills, and listening to their selection in a brain scanner (positron emission tomography) caused increased activity in the amygdala, hippocampus, and other structures associated with other euphoria-inducing stimuli such as food, sex, and drugs of abuse.

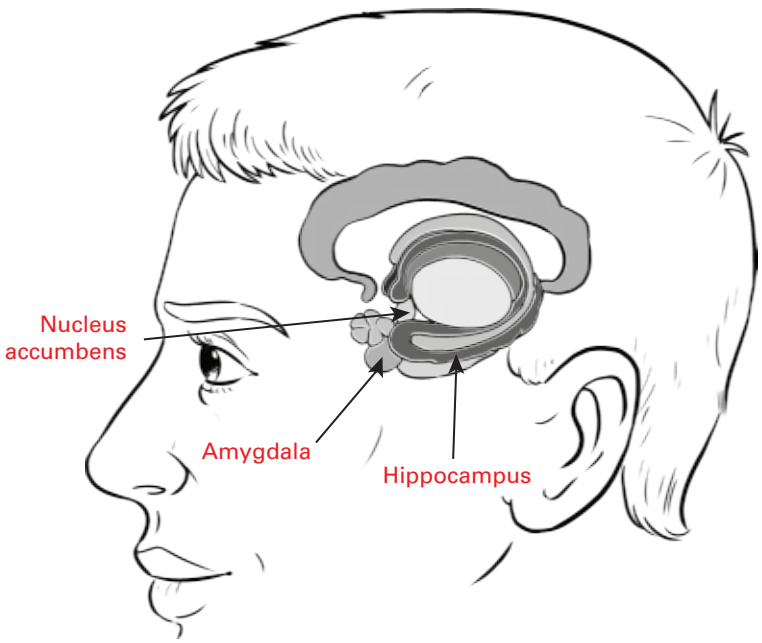

Figure 13.20 Three of the main structures deep in the brain that are involved in the recognition of emotions. There are others as well (see Figure 3.21).

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Figure 13.21, also based on imaging studies, shows how structures involved in music-elicited emotion structures are connected in a network. We can, therefore, think of music not only as activating many structures, but also as activating a network of structures that are communicating with each other (see Distributed Representation, Chapter 2, page 33).

Chemistry Because the intense emotions that can be elicited by music are highly rewarding, it isn't surprising that music-elicited emotions have been linked to activity in brain structures that are associated with behaviors like eating, sex, and the use of recreational drugs. One of these structures, the nucleus accumbens (NAcc) (see Figure 3.20), is closely associated with the neurotransmitter dopamine, which is released into the NAcc in response to rewarding stimuli (**Figure 3.22a**).

When Valorie Salimpoor and coworkers (2011) had participants rate the intensity of chills and pleasure as they listened to music, they found that more chills and pleasure were accompanied by greater activity in the NAcc (**Figure 3.22b**).

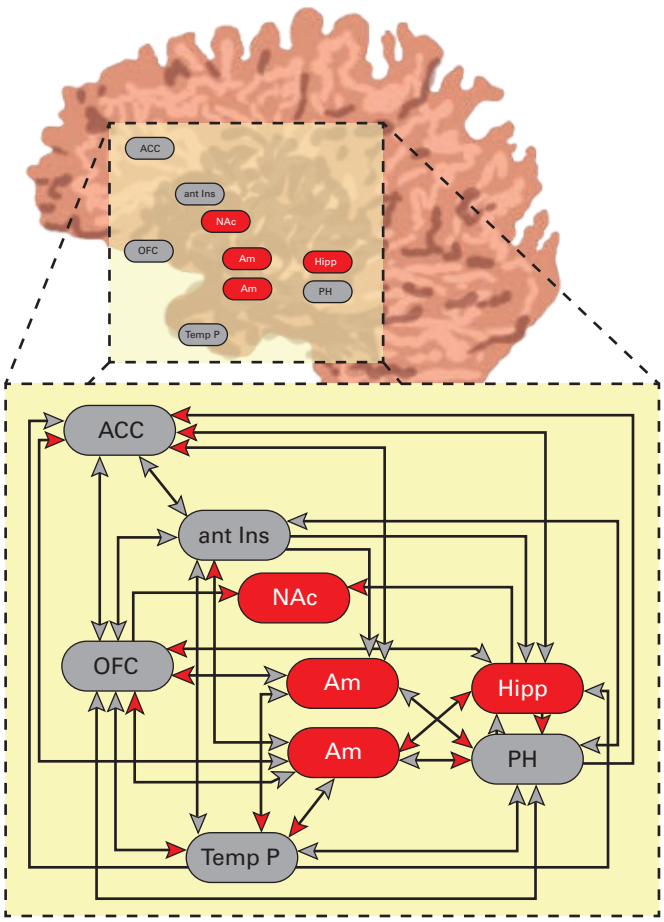

Figure 13.21 Connections between brain areas that are involved in the emotional processing of music. The hippocampus (Hipp), two areas in the amygdala (Am), and the nucleus accumbens (NAc), from Figure 13.20, are highlighted. The way these areas, plus others are connected to form a network is consistent with the idea that music, like other psychological responses, is based not only on which areas are involved, but on how areas communicate with each other.

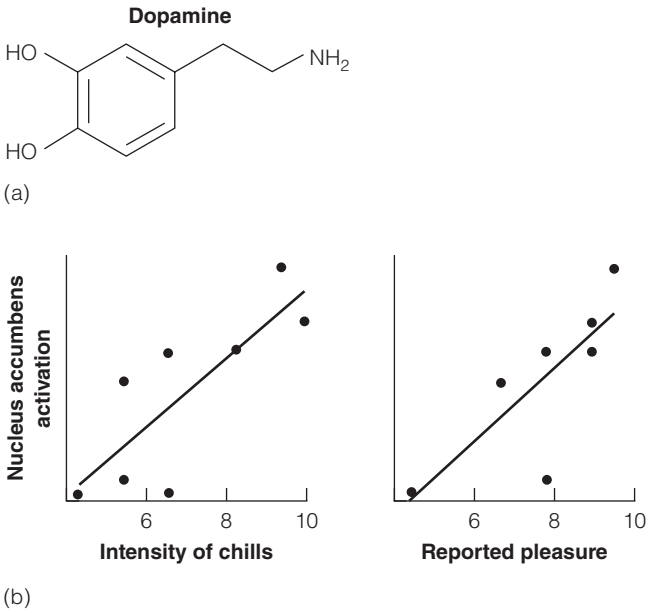

Figure 13.22 (a) The structure of dopamine, which plays an important role in creating music-elicited emotions. (b) The results of Salimpoor and coworkers' (2011) experiment, which shows that higher intensity of chills and reported pleasure are associated with higher activity in the nucleus accumbens, which is closely linked to the release of dopamine.

They concluded, based on this result, that the intense pleasure experienced when listening to music is associated with dopamine activity in the brain's reward system.

Another study on the chemistry of musical emotions showed that emotional responses to music were reduced when participants were given the drug naltrexone, which counteracts the effect of pleasure-inducing opioids (Mallik et al., 2017). They concluded that the opioid system is one of the chemical systems responsible for positive and negative responses to music. This relates to our discussion of dopamine, because it has been shown that blocking the opioid system reduces dopamine activity. Should we conclude from the above results that music is a drug? Perhaps, or to be more accurate, we can say that music can cause the release of mind-altering drugs (Ferreri et al., 2019).

Neuropsychology Finally, neuropsychological research has linked brain damage to deficits in music-elicited emotions. People with damage to their amygdala don't experience the pleasurable musical "chill" response (Griffiths et al., 2004) and can't recognize the emotions usually associated with scary music (Gosselin et al., 2005). Patients who had damage to their parahippocampus (an area surrounding the hippocampus) rated dissonant music, which normal controls found unpleasant, as being slightly pleasant (Gosselin et al., 2006).

One of the messages of research on brain structures involved in musical emotion is that there is overlap between the areas involved in music-evoked emotions and everyday emotions. As we will see in the next section, this overlap between "music" and "non-music" brain areas is not limited to emotions.

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SOMETHING TO CONSIDER:

Comparing Music and Language Mechanisms in the Brain

One of the major areas of research on music and the brain has focused on comparing music and language. This research is motivated by the fact that both language and music (Slevc, 2012)

1. are strings of sounds, linked together.
2. are unique to humans.
3. are found in all cultures.
4. can be combined in song.
5. involve creating expectations of what is to come.
6. have rhythm.
7. are organized according to rules of syntax (rules for how words or notes should be combined).
8. involve cooperation between people—conversation for language, playing in groups for music.

While music and language share many similarities, there are also differences:

1. Language can convey specific thoughts, based on the meaning of words and how they are arranged. Music doesn't have this capacity.
2. Music elicits emotions. This can occur for language, but isn't as central.
3. Music often repeats. This is less likely in language.
4. Music is often played in groups, whereas language is typically spoken by a single speaker.

Are these similarities and differences reflected in brain mechanisms? Interestingly, there is physiological evidence that supports both the idea that music and language are created by shared mechanisms and the idea that they are created by separate mechanisms.

Evidence for Shared Mechanisms

We've seen that violations of syntax in both music and language result in an electrical "surprise response" in the brain (Figure 13.18). This reflects the fact that key components of both music and language are predicting what is going to happen, and may make use of similar mechanisms. But we can't say, based on this finding alone, that music and language involve overlapping areas of the brain.

To look more directly at the brain, Patel and coworkers (2008) studied a group of stroke patients who had damage to Broca's area in the frontal cortex, which we will see in the next chapter that is important for perceiving speech (see Figure 14.17). This damage caused Broca's aphasia—difficulty in understanding sentences with complex syntax (see page 349). These patients and a group of controls were given (1) a language task that involved understanding syntactically complex sentences; and (2) a music task that involved detecting the off-key chords in a sequence of chords. The results of these tests, shown in **Figure 13.23**, indicate that the patients performed poorly on the language task compared to the controls (left pair of bars), and that the patients also performed more poorly on the music task (right pair of bars). Two things that are noteworthy about these results are: (1) there is a connection between poor performance on the language task and poor performance on the music task, which suggests a connection between the two; and (2) the deficits in the music task for aphasia patients were small compared to the deficits in the language tasks. These results support a connection between brain mechanisms involved in music and language, but not necessarily a strong connection.

Brain mechanisms have also been studied using neuroimaging. Some of these studies have shown that different areas are involved in music and language (Fedorenko et al., 2012). Other studies have shown that music and language activate overlapping areas of the brain. For example, Broca's area, which is involved in language syntax, is also activated by music (Fitch & Martins, 2014; Koelsch, 2005, 2011; Kunert et al., 2015; Peretz & Zatorre, 2005).

It is important, however, to realize the limitations of neuroimaging results. Just because neuroimaging identifies an area that is activated by both music and language, this doesn't necessarily mean that music and language are activating the same neurons within that area. There is evidence that even if music and language activate the same area, this activation can involve different neural networks (**Figure 13.24**) (Peretz et al., 2015).

Evidence for Separate Mechanisms

In the previous section we saw that the study of patients with brain damage provides some evidence for shared mechanisms. But the effects of brain damage also provide evidence for separate mechanisms. One of the techniques for determining separate mechanisms is determining a double dissociation (see Method: Double Dissociations in Neuropsychology, Chapter 4,

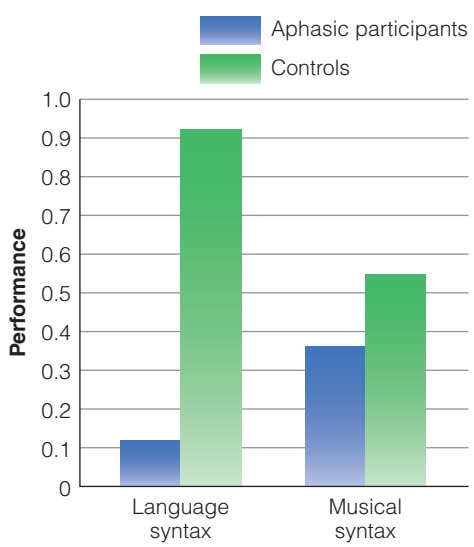

Figure 13.23 Performance on language syntax and musical syntax tasks for aphasic participants and control participants.

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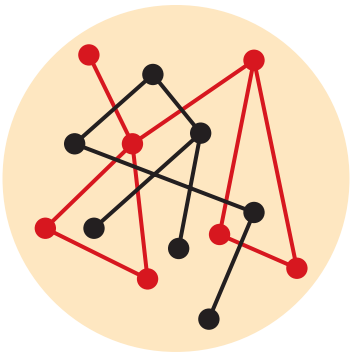

Figure 13.24 Illustration of the idea that two different capacities, such as language and music, might activate the same structure in the brain (indicated by the circle), but when looked at closely, each capacity could activate different networks (red or black) within the structure. The small circles represent neurons, and the lines represent connections.

page 81). For the music versus language question, that would involve finding one person who is deficient in perceiving music but has normal language abilities and another person who is deficient in language but has normal musical abilities.

People with a condition called **congenital amusia** don't recognize tones as tones, and therefore do not experience sequences of tones as music (Peretz, 2006). Oliver Sacks, in his book *Musicophilia: Tales of Music and the Brain* (2007) describes the case of D.L., a 76-year-old woman who had trouble singing and identifying tunes. She couldn't tell whether one note was higher than another, and when asked what she heard when music was played, she answered, "If you were in my kitchen and threw all of the plates and pans on the floor, that's what I hear." But despite her amusia, she had no trouble hearing, remembering, or enjoying other sounds, including speech. The opposite effect has been observed in patients who suffered brain damage as adults who have lost the ability to recognize words but can still recognize music (Fitch & Martins, 2014; Peretz, 2006).

A recent laboratory experiment that studied both behavioral and physiological differences between music and speech was carried out by Philippe Albouy and coworkers (2020), who had participants listen to songs being sung *a capella* (an unaccompanied solo voice). The listeners were presented with pairs of songs, and their task was to determine whether their words were the same or different, or, in another task, if their melody was the same or different. This task was easy when the listeners were presented with unaltered songs. However, it became more difficult when the songs were degraded.

The key feature of this experiment is that the songs were degraded in two different ways. Removing *temporal details* involved changing the timing (fast–slow) of the sounds. Removing *spectral details* involved changing the sound frequency (high–low) of the sounds. Which type of degradation do you think affected the ability to recognize the words?

The answer is that recognizing words often depends on split-second timing of the speech signal, which, for example, helps us tell the difference between similar sounding words like *bear* and *pear*. However, changing the frequency has little effect on word recognition, which makes sense when we consider that we can recognize words when spoken by either high-pitched or low-pitched voices.

In contrast, the opposite happens for melodies. Changing spectral details affects melodies, but changing the timing has little effect. This also makes sense when we consider how melodies depend on the vertical (high–low) position of notes on the musical score, but when we hear different interpretations of songs, which often involve changing the pacing or timing of the notes, we can still recognize the melody.

The results of this experiment are shown in **Figure 13.25**. Notice that changes in temporal information (**Figure 13.25a**)

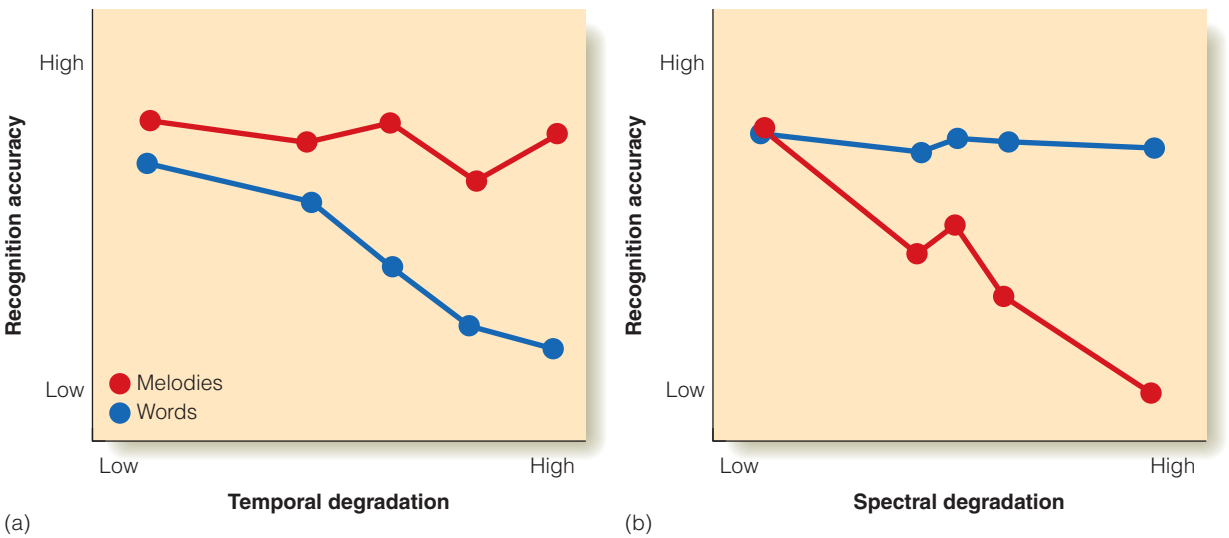

Figure 13.25 The results of Albouy and coworkers' (2020) experiment in which the effect of temporal degradation or spectral degradation of songs was measured for words and for melodies. (a) Temporal degradation decreases word recognition but has little effect on melody recognition. (b) Spectral degradation decreases melody recognition but has little effect on word recognition.

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had little effect on the ability to recognize melodies, but had a large effect on recognizing words, whereas the opposite happened when spectral information was changed (**Figure 13.25b**).

This difference between speech and music becomes even more interesting when we consider the second part of Albouy's experiment, in which she used fMRI to determine how brain activity was affected by temporal or spectral degradation and found that changes in the temporal pattern, which had affected sentence recognition, had a large effect on the response of the left hemisphere of the brain, whereas changes in the spectral pattern had a large effect on the response of the right hemisphere.

Based on these differences, Albouy concluded that humans have developed two forms of auditory communication, speech and music, and that each of these forms are served by specialized neural systems that operate in different hemispheres. The advantage of this separation is that separate areas are available for encoding the different types of sounds involved in music and speech. In the next chapter, we will consider the speech signal and how we understand it.

The conclusion from all of these studies—both behavioral and physiological—is that while there is evidence that music and language share mechanisms, there is also evidence for separated mechanisms. Thus, it seems that the brain processes involved in music and language are related, but the overlap isn't complete, as might be expected when you consider the difference between reading a book or listening to a conversation and listening to music. Clearly, our knowledge of the relation between music and language is still a work in progress (Eggermont, 2014).

DEVELOPMENTAL DIMENSION How Infants Respond to the Beat

Infants love music! They are soothed by mother's lullabies (Cirelli et al., 2019) and hearing music keeps them from becoming distressed (Corbeil et al., 2016; Trehub et al., 2015). But how do infants and young children respond to the two components of music, timing and melody?

Newborns' Response to the Beat

How can we tell if a newborn can detect the beat in music? István Winkler and coworkers (2009) answered this question by measuring electrical brain responses of 2- to 3-day-old infants as they listened to short sequences of sounds created by a drum, bass, and hi-hat (**Figure 13.26**). The "standard" pattern contained a constant beat of 1 2 3 4 1 2 3 4 by the hi-hat, with supporting beats by the drum and bass. But occasionally omitting the downbeat (the first beat in a measure) caused electrical activity associated with violating expectations. It appears, therefore, that newborns can perceive the beat.

Dr. Gábor Stefanics

Figure 13.26 Two-day-old infant having brain activity recorded while listening to "the beat." Brain responses are recorded by electrodes pasted onto the scalp. The electrode on the nose is the reference electrode. (Photo courtesy of István Winkler and Gabor Stefanics)

Older Infants' Movement to the Beat

Newborns don't move to the beat, but there is evidence that older infants do. When 5- to 24-month-old infants' movements were videotaped as they listened to rhythmic classical music or speech, it was found that they moved their arms, hands, legs, torso, and head in response to the music more than when they were listening to speech. The infants were sitting on their mothers' laps during this experiment, so the ones who could stand weren't "dancing." But there was some synchronization between the movements and the music, and the researchers point out that more synchrony might have occurred to music with a more pronounced beat than what the infants heard in this experiment. (Check out "baby dancing" on YouTube for some entertaining examples.)

Infants' Response to Bouncing to the Beat

Responses to the beat have also been demonstrated by bouncing infants in synchrony with the beat, similar to the adult bouncing experiment described on page 317, which showed that movement can affect the perception of meter. As 7-month-old infants listened to a regular repeating rhythm that had no accents, they were bounced up and down (**Figure 13.27**) (Phillips-Silver & Trainor, 2005). These bounces occurred either in a duple pattern (a bounce on every second beat) or in a triple pattern (a bounce on every third beat). After being bounced for 2 minutes, the infants were tested to determine

Continued

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Zackery Pierce

Figure 13.27 A mother (and co-author of this book) bouncing her son up and down, as was done in Phillips-Silver and Trainor's (2005) experiment, in which infants were bounced on either every second beat or on every third beat.

whether this movement caused them to hear the regular pattern in groups of two or in groups of three. The researchers used a head-turning preference procedure to determine whether the infants preferred listening to a pattern that had accents that corresponded to how they had been bounced.

METHOD | Head-Turning Preference Procedure

In the preference technique, an infant sitting on the mother's lap has his or her attention directed to a flashing light illuminating a visual display. When the infant looks at the light, it stays on and the infant hears a repeating sound, which is accented to create either a duple or a triple pattern. The infant continues to hear one of these patterns while he or she is looking at the light. When the infant looks away, the sound goes off. This is done for a number of trials, and the infant quickly learns that looking at the light keeps the sound on. Thus, the question of whether the infant prefers the duple or triple pattern can be answered by determining which sound the infant chooses to listen to longer.

Phillips-Silver and Trainor found that infants listened to the pattern they had been bounced to for an average of 8 seconds but only listened to the other pattern for an average of 6 seconds. The infants therefore preferred the pattern they had been bounced to. To determine whether this effect was due to vision, infants were bounced while blindfolded. (Although the infants loved being bounced, they weren't so thrilled about being blindfolded!) The result, when they were tested later using the head-turning procedure, was the same as when they could see, indicating that vision was not a factor. Also, when the infants just watched the experimenter bounce, the effect didn't occur. Apparently *moving* is the key to influencing metrical grouping.

The experiments we've described have focused on the beginnings of the infant's ability to respond to the beat. This development continues into childhood, until eventually, some people become experts at relating to the beat, either through dancing to music or making music, and just about everybody becomes expert at listening to and reacting to the beat.

13.7 Coda: Music Is "Special"

This chapter, like all the others in this book, is about perception. For music, perception is concerned with how tones arranged in a certain pattern and with certain timing are perceived as "music." One way to think about the transformation of sounds into the perception of music is to draw parallels between perceiving music and perceiving visual stimuli. Perceiving music depends on how sounds are arranged plus our expectations drawn from prior experience with musical sounds. Similarly, visual perception depends on the arrangement of visual stimuli plus our expectations based on past experiences with visual stimuli.

But despite these similarities, there is something special about music, because while perception is the first step, other things happen that extend beyond perception, with movement and emotion at the top of the list. Think about what this means when we compare music to vision. We know that movement is an important aspect of vision. We not only perceive movement (Chapter 8), but vision depends on movements of our body and eyes to direct our attention (Chapter 6), and vision helps us direct movements that are necessary for us to take action and interact with the environment (Chapter 7). In fact, in Chapter 7 we introduced the idea that the primary purpose of the brain is to allow organisms to interact with the environment (p. 147).

So how does the movement that accompanies music compare to vision's impressive list of movement-related functions? One answer to this question is that whereas vision *enables* us to direct our movements, music *compels* us to move, especially when music has a strong beat or is syncopated.

Another aspect of music—emotion—also occurs in response to vision, when looking at a beautiful sunset or art, or seeing joyful or disturbing events, elicit emotions, but this occurs only occasionally. We are usually just seeing what's out there, without necessarily experiencing emotions, whereas emotion is a *central* characteristic of music.

So when compared to vision, music seems special because of its stronger link to movement and emotions. Other perceptual qualities associated with emotions are pain (Chapter 15) and taste and smell (Chapter 16). However, in contrast to music, the emotions associated with pain, taste, and smell are considered to have adaptive value by helping us avoid

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dangerous stimuli, and, in the case of taste and smell, also by helping us seek out rewarding stimuli.

This brings us back to the question "what is music for?" from the beginning of the chapter. In connection with this, let's return to Charles Darwin, who, although suggesting that music may have laid the foundation for language, and is helpful in attracting sexual partners (p. 312), seemed uncertain as to the "why" of music, as indicated by the following statement in his famous book *The Descent of Man* (1871):

> As neither the enjoyment nor the capacity of producing musical notes are faculties of the least direct use to man..., they must be ranked among the most mysterious with which he is endowed.

But Robert Zatorre (2018) noted, in a presentation titled "From Perception to Pleasure: Musical Processing in the Brain," that in Darwin's autobiography, which was written ten years after *The Descent of Man*, he makes the following statement about music:

> If I were to live my life again, I would have made a rule to read some poetry and listen to some music at least once every week, so perhaps the parts of my brain now atrophied, would thus have been kept active through use.... The loss of these tastes is the loss of happiness and may possibly be injurious to the intellect and to the moral character by enfeebling the emotional part of our nature.

What does this mean? Zattore suggests that, even though Darwin may have been uncertain as to the purpose of music, he is saying that without music, life is unpleasant and empty. Thus, music raises many questions beyond how it is perceived, and that is what makes it something special.

TEST YOURSELF 13.2

1. Contrast the cognitivist approach and the emotivist approach to music-elicited emotions.
2. Describe how structural features of music are linked to emotions.
3. What causes expectations in music?
4. Describe the event-related potential. How does it respond both in language and music to violations of syntax?
5. Why would composers want to violate a listener's expectations?
6. Describe evidence for physiological mechanisms of music-elicited emotions determined by (a) measuring electrical responses; (b) determining which structures are activated; (c) looking at the chemistry of music-elicited emotions; (d) neuropsychological research.
7. Compare music and language, indicating similarities and differences.
8. What is the evidence supporting the idea that music and language involve separate brain mechanisms?
9. What is the evidence for shared mechanisms for music and language? Describe Patel's experiment, Broca's aphasia experiment, and neuroimaging evidence.
10. What is the overall conclusion, taking the evidence for and against shared mechanisms between music and language into account?
11. What is the evidence that newborns and older infants can respond to the beat?
12. How is music "special" when compared to vision?
13. What did Darwin say about music that indicates it is special?

THINK ABOUT IT

1. It is well known that young people prefer pop music over classical music, and that the popularity of classical music increases as listeners get older. Why do you think this is?
2. If you were stranded on a desert island and could only listen to a dozen musical compositions, which would you pick? What special properties do these compositions have that caused you to put them on your list?
3. Do you or have you ever made music by playing an instrument or singing? What do you get out of making music? How does that relate to what you get out of listening to music?

KEY TERMS

Arch trajectory (p. 320)
Beat (p. 315)
Broca's aphasia (p. 327)
Cloze probability task (p. 320)
Cognitivist approach (to musical emotion) (p. 321)
Congenital amusia (p. 328)
Consonance (p. 312)
Dissonance (p. 312)
Dopamine (p. 326)
Duple meter (p. 316)
Early right anterior negativity (ERAN) (p. 325)
Emotivist approach (to musical emotion) (p. 321)
Event-related potential (ERP) (p. 323)
Evolutionary adaptation (p. 312)
Gap fill (p. 319)
Harmony (p. 312)
Inter-onset interval (p. 316)
Interval (p. 319)
Melody (p. 312)
Meter (p. 315)
Metrical structure (p. 316)

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Music (p. 311)
Music-evoked autobiographical memory (MEAM) (p. 313)
Musical phrases (p. 319)
Musical syntax (p. 323)
Nucleus accumbens (p. 326)
Pitch (p. 312)
Return to the tonic (p. 320)
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Semitone (p. 319)
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Syntax (p. 323)
Temporal structure (p. 312)
Timbre (p. 312)
Tonal hierarchy (p. 320)
Tonality (p. 320)
Tonic (p. 320)
Triple meter (p. 316)
Vestibular system (p. 318)

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This communication between father and son is based on understanding spoken language, which depends on how our perceptual system transforms spoken sounds into the perception of words and sequences of words, and on how cognitive processes help us interpret what we are hearing.

Porta/DigitalVision/Getty Images

Learning Objectives

After studying this chapter, you will be able to ...

- Describe how the acoustic signal is created by the action of articulation and is represented by phonemes.
- Understand the processes responsible for variability in the acoustic signal.
- Describe the motor theory of speech perception and evidence for and against the theory.
- Describe the multiple sources of information for speech perception.
- Understand how people perceive degraded speech.
- Describe how research involving brain damage and neural recording has contributed to our understanding of how speech is processed by the brain.
- Understand how cochlear implants work and how they have been used in children.
- Describe infant-directed speech and how it affects infants.

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CHAPTER 14

Perceiving Speech

CHAPTER CONTENTS

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The Acoustic Signal
Basic Units of Speech

14.2 Variability of the Acoustic Signal
Variability From Context
Variability in Pronunciation

14.3 Some History: The Motor Theory of Speech Perception
The Proposed Connection Between Production and Perception
The Proposal That "Speech Is Special"

TEST YOURSELF 14.1

14.4 Information for Speech Perception
Motor Processes
The Face and Lip Movements
Knowledge of Language
The Meaning of Words in Sentences

DEMONSTRATION: Perceiving Degraded Sentences

DEMONSTRATION: Organizing Strings of Sounds
Learning About Words in a Language

TEST YOURSELF 14.2

14.5 Speech Perception in Difficult Circumstances

14.6 Speech Perception and the Brain

SOMETHING TO CONSIDER: Cochlear Implants

DEVELOPMENTAL DIMENSION: Infant-Directed Speech

TEST YOURSELF 14.3

THINK ABOUT IT

Some Questions We Will Consider:

- Can computers perceive speech as well as humans? (p. 335)
- Is each sound we hear associated with a specific pattern of air pressure changes? (p. 338)
- Why does an unfamiliar foreign language often sound like a continuous stream of sound, with no breaks between words? (p. 345)
- What does a person with a cochlear implant hear compared to a person with normal hearing? (p. 352)

Although we perceive speech easily under most conditions, beneath this ease lurks processes as complex as those involved in perceiving the most complicated visual scenes. One way to appreciate this complexity is to consider attempts to use computers to recognize speech, a process called **automatic speech recognition (ASR)**.

Attempts to create ASR systems began in the 1950s, when Bell Laboratories designed the "Audrey" system, which could recognize single spoken digits. Many decades of work, combined with vastly improved computer technology, culminated in the introduction of ASR systems like Apple's *Siri*, Amazon's *Alexa*, and Google's *Voice*, which do a good job of recognizing spoken commands.

However, *Siri*, *Alexa*, and *Voice* notwithstanding, the performance of modern ASR systems ranges from very good, under ideal conditions, when ASR can create printed transcriptions of spoken language with as high as 95 percent accuracy (Spille et al., 2018), to not so good, under less than ideal conditions. For example, Adam Miner and coworkers (2020) had a person listen to a recording of a two-person conversation in which the microphone was not optimally placed and there was noise in the room. Despite the microphone placement and the noise, the person was able to create an accurate written transcription of the conversation. However, when an ASR device created a transcript from the same recording, it made mistakes such as identifying words incorrectly, missing words, and inserting words that weren't said, so that only 75 percent of the words were correct. Other experiments have shown that ASR systems make errors when confronted with accents and non-standard speech patterns (Koenecke et al., 2020).

Thus, while ASR has come a long way since the 1950s, 70 years of development has resulted in computer speech recognition systems that still fall short of human listeners, who can perceive speech even when confronted with phrases they have never heard, and under a wide variety of conditions,

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including the presence of various background noises, variations in pronunciation, speakers with different dialects and accents, and the often chaotic give-and-take that routinely occurs when people talk with one another (Huang et al., 2014; Sinha, 2002). This chapter will help you appreciate the complex perceptual problems posed by speech and will describe research that has helped us begin to understand how the human speech perception system has solved some of these problems.

14.1 The Speech Stimulus

Chapter 11 introduced pure tones—simple sine-wave patterns with different amplitudes and frequencies, and then complex tones—a number of pure tones, called harmonics, occurring together, with frequencies that are multiples of the tone's fundamental frequency. The sounds of speech increase the complexity one more level. We can still describe speech in terms of frequencies, but a complete description needs to take into account abrupt starts and stops, silences, and noises that occur as speakers form words. It is these words that enable speakers to create meaning by saying words and stringing them together into sentences. These meanings, in turn, influence our perception of the incoming stimuli, so that what we perceive depends not only on the physical sound stimulus but also on cognitive processes that help us interpret what we are hearing. We begin by describing the physical sound stimulus, called the *acoustic signal*.

The Acoustic Signal

Speech sounds are produced by the position or the movement of structures within the vocal apparatus, which creates patterns of pressure changes in the air called the **acoustic stimulus**, or the **acoustic signal**. The acoustic signal for most speech sounds is created by air that is pushed up from the lungs past the vocal cords and into the vocal tract. The sound that is produced depends on the shape of the vocal tract as air escaping from the lungs is pushed through it. The shape of the vocal tract is altered by moving the **articulators**, which include structures such as the tongue, lips, teeth, jaw, and soft palate (**Figure 14.1**).

Let's first consider the production of vowels. Vowels are produced by vibration of the vocal cords, and the specific sounds of each vowel are created by changing the overall shape of the vocal tract. This change in shape changes the resonant frequency of the vocal tract and produces peaks of pressure at a number of different frequencies (**Figure 14.2**). The frequencies at which these peaks occur are called **formants**.

Each vowel sound has a characteristic series of formants. The first formant has the lowest frequency; the second formant is the next highest; and so on. The formants for the vowel /ae/ (the vowel sound in the word *had*) are shown on a **sound spectrogram** in **Figure 14.3** (speech sounds are indicated by setting them off with slashes). The sound spectrogram

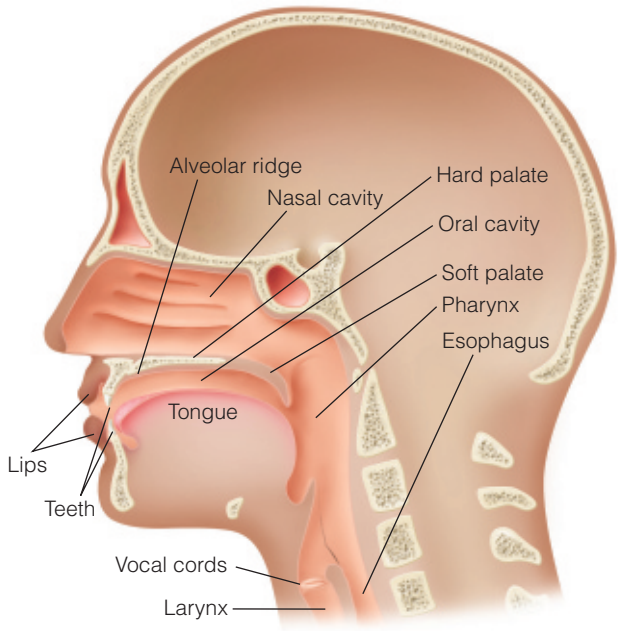

Figure 14.1 The vocal tract includes the nasal and oral cavities and the pharynx, as well as components that move, such as the tongue, lips, and vocal cords.

indicates the pattern of frequencies and intensities over time that make up the acoustic signal. Frequency is indicated on the vertical axis and time on the horizontal axis; intensity is

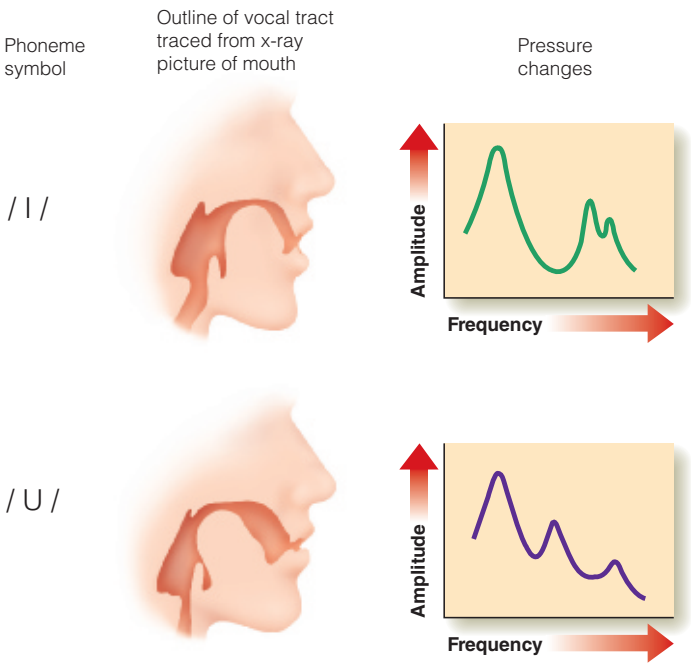

Figure 14.2 Left: the shape of the vocal tract for the vowels /I/ (as in *zip*) and /U/ (as in *put*). Right: the amplitude of the pressure changes produced for each vowel. The peaks in the pressure changes are the *formants*. Each vowel sound has a characteristic pattern of formants that is determined by the shape of the vocal tract for that vowel. (From Denes & Pinson, 1993)

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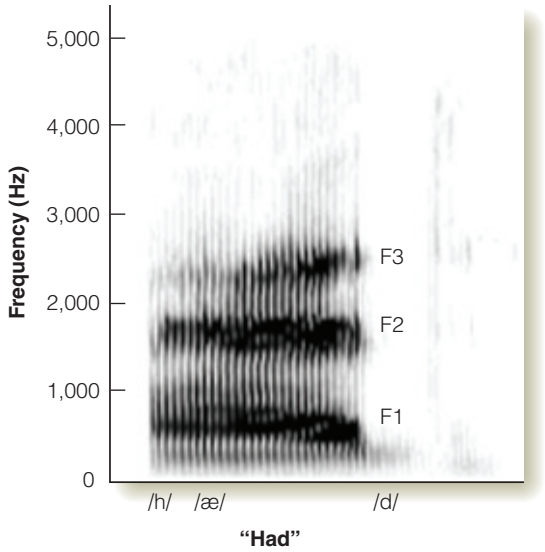

Figure 14.3 Spectrogram of the word *had*. "Time" is on the horizontal axis. The dark horizontal bands are the first (F1), second (F2), and third (F3) formants associated with the sound of the vowel /ae/. (Spectrogram courtesy of Kerry Green)

indicated by darkness, with darker areas indicating greater intensity. From Figure 14.3 we can see that formants are concentrations of energy at specific frequencies, with the sound /ae/ having formants at 500, 1,700, and 2,500 Hz, which are labeled F1, F2, and F3 in the figure. The vertical lines in the spectrogram are pressure oscillations caused by vibrations of the vocal cord.

Consonants are produced by a constriction, or narrowing, of the vocal tract. To illustrate how different consonants are produced, let's focus on the sounds /g/, /d/, and /b/. Make these sounds, and notice what your tongue, lips, and teeth are doing. As you produce the sound /d/, you place your tongue against the ridge above your upper teeth (the alveolar ridge of Figure 14.1) and then release a slight rush of air as you move your tongue away from the alveolar ridge (try it). As you produce the sound /b/, you place your two lips together and then release a burst or air.

The way speech sounds are produced is described by characteristics that include the *manner of articulation* and the *place of articulation*. The **manner of articulation** describes how the articulators—the mouth, tongue, teeth, and lips—interact when making a speech sound. For example, /b/ is created by blocking the airflow and releasing it quickly. The **place of articulation** describes the locations of the articulation. Notice, for example, how the place of articulation moves from the back to the front of the mouth as you say /g/, /d/, and /b/.

Movements of the tongue, lips, and other articulators create patterns of energy in the acoustic signal that we can observe on the sound spectrogram. For example, the spectrogram for the sentence "Roy read the will," shown in **Figure 14.4**, shows aspects of the signal associated with vowels and consonants. The three horizontal bands marked F1, F2, and F3 are the three formants associated with the /e/ sound of *read*. Rapid shifts in frequency preceding or following formants are called **formant transitions** and are associated with consonants. For example, T2 and T3 in Figure 14.4 are formant transitions associated with the /r/ of *read*.

We have described the physical characteristics of the *acoustic signal*. To understand how this acoustic signal results in *speech perception*, we need to consider the basic units of speech.

Basic Units of Speech

Our first task in studying speech perception is separating the acoustic stream of speech into linguistic units that reflect the listener's perceptual experience. What are these units? The flow of a sentence? A particular word? A syllable? The sound of a letter? A sentence is too large a unit for easy analysis, and some letters have no sounds at all. Although there are arguments for the idea that the syllable is the basic unit of speech (Mehler, 1981; Segui, 1984), most speech research has been

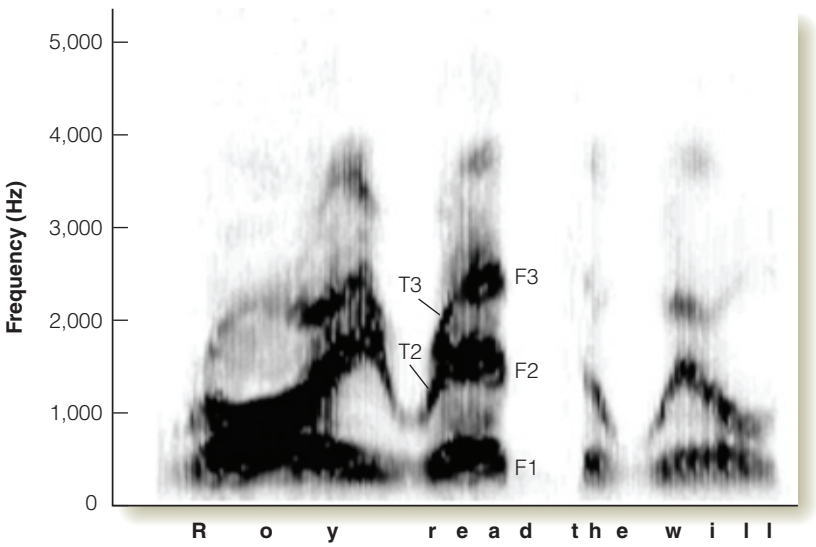

Figure 14.4 Spectrogram of the sentence "Roy read the will," showing formants F1, F2, and F3 and formant transitions T2 and T3. (Spectrogram courtesy of Kerry Green)

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based on a unit called the **phoneme**. A phoneme is the shortest segment of speech that, if changed, would change the meaning of a word. Consider the word *bit*, which contains the phonemes /b/, /i/, and /t/. We know that /b/, /i/, and /t/ are phonemes because we can change the meaning of the word by changing each phoneme individually. Thus, *bit* becomes *pit* if /b/ is changed to /p/, *bit* becomes *bat* if /i/ is changed to /a/, and *bit* becomes *bid* if /t/ is changed to /d/.

The phonemes of American English, listed in **Table 14.1**, are represented by phonetic symbols that stand for speech sounds. This table shows phonemes for 13 vowel sounds and 24 consonant sounds. Your first reaction to this table may be that there are more vowels than the standard set you learned in grade school (*a*, *e*, *i*, *o*, *u*, and sometimes *y*). The reason there are more vowels is that some vowels can have more than one pronunciation, so there are more vowel sounds than vowel letters. For example, the vowel *o* sounds different in *boat* and *hot*, and the vowel *e* sounds different in *head* and *heed*. Phonemes, then, refer not to letters but to speech sounds that determine the meaning of what people say.

Because different languages use different sounds, the number of phonemes varies across languages. There are only 13 phonemes in Hawaiian, but as many as 47 have been identified in American English and up to 60 in some African languages. Thus, phonemes are defined in terms of the sounds that are used to create words in a specific language.

It might seem that if the phoneme is the basic unit of speech, we could describe speech perception in terms of strings of phonemes. According to this idea, we perceive a series of sounds called phonemes, which create syllables that combine to create words. These syllables and words appear strung together one after another like beads on a string. For example, we perceive the phrase "perception is easy" as the sequence of units "per-sep-shun-iz-ee-zee."

Although perceiving speech may seem to be just a matter of processing a series of discrete sounds that are lined up one after another, the actual situation is much more complex. Rather than following one another, with the signal for one sound ending and then the next beginning, like letters on a page, signals for neighboring sounds overlap one another. A further complication is that the acoustic signal for a particular word can vary greatly depending on whether the speaker is male or female, young or old, speaks rapidly or slowly, or has an accent. This creates the **variability problem**, which refers to the fact that there is no simple relationship between a particular phoneme and the acoustic signal. In other words, the acoustic signal for a particular phoneme is variable. We will now describe a number of ways that this variability occurs and an early attempt to deal with this variability.

Table 14.1 Major Consonants and Vowels of English and Their Phonetic Symbols

CONSONANTS				VOWELS	
p	*p*ull	s	*s*ip	i	h*ee*d
b	*b*ull	z	*z*ip	I	h*i*d
m	*m*an	r	*r*ip	e	b*ai*t
w	*w*ill	š	*sh*ould	ɛ	h*ea*d
f	*f*ill	ž	plea*s*ure	æ	h*a*d
v	*v*et	č	*ch*op	*u*	wh*o'*d
θ	*th*igh	ǰ	*g*yp	U	p*u*t
ð	*th*at	y	*y*ip	^	b*u*t
t	*t*ie	k	*k*ale	o	bo*a*t
d	*d*ie	g	*g*ale	O	bo*ug*ht
n	*n*ear	h	*h*ail	a	h*o*t
l	*l*ear	*ŋ*	si*ng*	ə	sof*a*

There are other American English phonemes in addition to those shown here, and specific symbols may vary depending on the source.

14.2 Variability of the Acoustic Signal

The main problem facing researchers trying to understand speech perception is that there is a variable relationship between the acoustic signal and perception of that signal. Thus, a particular phoneme can be associated with a number of different acoustic signals. Let's consider some of the sources of this variability.

Variability From Context

The acoustic signal associated with a phoneme changes depending on its context. For example, look at **Figure 14.5**, which shows spectrograms for the sounds /di/ and /du/. These are smoothed hand-drawn spectrograms that show the two most important characteristics of the sounds: the formants (shown in red) and the formant transitions (shown in blue). Because formants are associated with vowels, we know that the

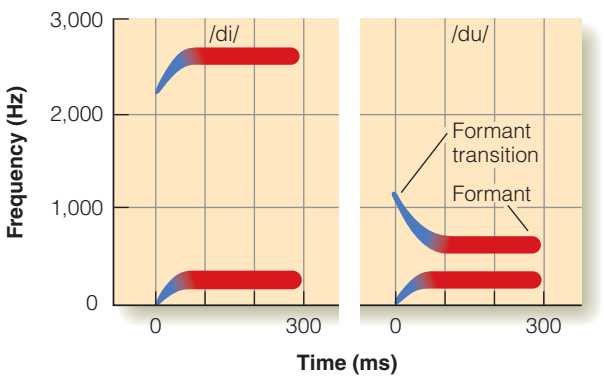

Figure 14.5 Hand-drawn spectrograms for /di/ and /du/. (From Liberman et al., 1967)

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formants at 200 and 2,600 Hz are the acoustic signal for the vowel /i/ in /di/ and that the formants at 200 and 600 Hz are the acoustic signal for the vowel /u/ in /du/.

Because the formants are associated with the vowels, the formant transitions that precede the vowel-related steady-state formants must be the signal for the consonant /d/. But notice that the formant transitions for the second (higher-frequency) formants of /di/ and /du/ are different. For /di/, the formant transition starts at about 2,200 Hz and rises to about 2,600 Hz. For /du/, the formant transition starts at about 1,100 Hz and falls to about 600 Hz. Thus, even though we perceive the same /d/ sound in /di/ and /du/, the formant transitions, which are the acoustic signals associated with these sounds, are very different. Thus, the context in which a specific phoneme occurs can influence the acoustic signal that is associated with that phoneme (McRoberts, 2020).

This effect of context occurs because of the way speech is produced. Because articulators are constantly moving as we talk, the shape of the vocal tract associated with a particular phoneme is influenced by the sounds that both precede and follow that phoneme. This overlap between the articulation of neighboring phonemes is called **coarticulation**. You can demonstrate coarticulation to yourself by noting how you produce phonemes in different contexts. For example, say *bat* and *boot*. When you say *bat*, your lips are unrounded, but when you say *boot*, your lips are rounded, even during the initial /b/ sound. Thus, even though the /b/ is the same in both words, you articulate each differently. In this example, the articulation of /oo/ in *boot* overlaps the articulation of /b/, causing the lips to be rounded even before the /oo/ sound is actually produced.

The fact that we perceive the sound of a phoneme as the same even though the acoustic signal is changed by coarticulation is an example of *perceptual constancy*. This term may be familiar to you from our observations of constancy phenomena in the sense of vision, such as color constancy (we perceive an object's chromatic color as constant even when the wavelength distribution of the illumination changes, page 215) and size constancy (we perceive an object's size as constant even when the size of its image changes on our retina, page 250). Perceptual constancy in speech perception is similar. We perceive the sound of a particular phoneme as constant even when the phoneme appears in different contexts that change its acoustic signal.

Variability in Pronunciation

People say the same words in a variety of different ways. There are *between speaker differences*—variations in how different people say words. Some people's voices are high-pitched and some are low-pitched; people speak with various accents; some talk very rapidly and others speak e-x-t-r-e-m-e-l-y s-l-o-w-l-y. These wide variations in speech mean that for different speakers, a particular phoneme or word can have very different acoustic signals. Analysis of how people actually speak has determined that there are 50 different ways to produce the word *the* (Waldrop, 1988).

There are also *within speaker differences*—variations in how an individual speaker says words. When talking to a friend "This was a best buy" might come out "This was a bes buy," with the /t/ being omitted. Or "Did you go to the store?" might come out "Didjoo go to the store?" However, you might speak more slowly and formally if you were talking to a teacher, pronouncing the /t/ in "best buy" and by saying "Did you" as two separate words.

That people do not usually articulate each word individually in conversational speech is reflected in the spectrograms in **Figure 14.6**. The spectrogram in **Figure 14.6a** is for the question "What are you doing?" spoken slowly and distinctly; the spectrogram in **Figure 14.6b** is for the same question taken from conversational speech, in which "What are you doing?" becomes "Whad'aya doin'?" This difference shows up clearly in the spectrograms. Although the first and last words (*what* and *doing*) create similar patterns in the two spectrograms, the pauses between words are absent or are much less obvious in the spectrogram of Figure 14.6b, and the middle of this spectrogram is completely changed, with a number of speech sounds missing.

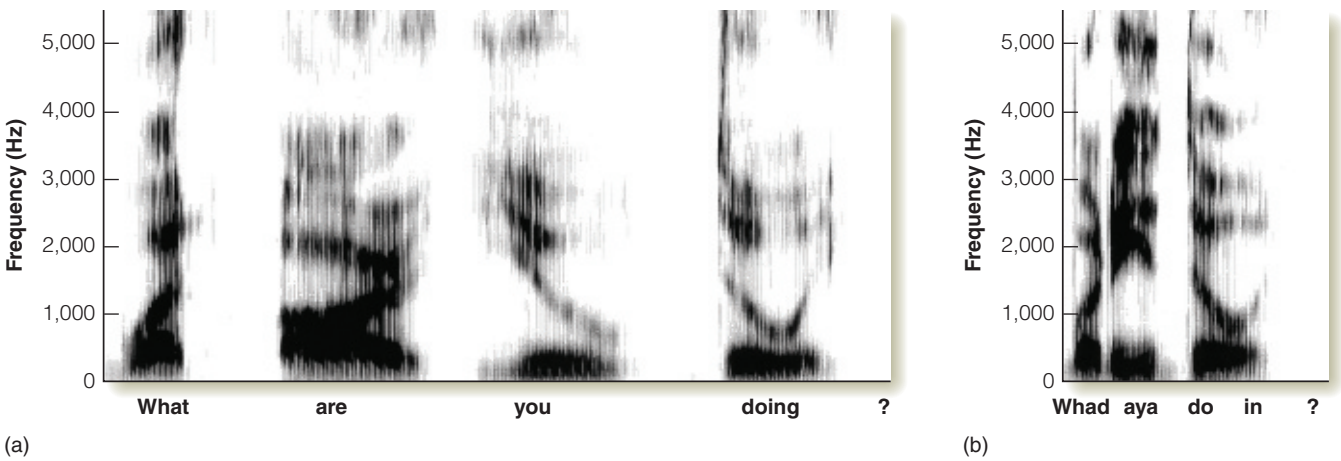

Figure 14.6 (a) Spectrogram of "What are you doing?" pronounced slowly and distinctly. (b) Spectrogram of "What are you doing?" as pronounced in conversational speech. (Spectrograms courtesy of David Pisoni)

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The variability in the acoustic signal caused by coarticulation and differences between and within speakers creates a problem for the listener, because there isn't a "standard" acoustic signal for each phoneme. In the next section, we will consider an early attempt to solve this problem.

14.3 Some History: The Motor Theory of Speech Perception

It was the 1960s, and researchers at the Haskins Laboratory in New York were working to develop a reading machine for the blind. The idea behind this machine was to capture the acoustic signals associated with the letters in each word and to transform that signal into sounds to create words (Whalen, 2019). As part of the project, the Haskins researchers had developed a machine called the **speech spectrograph**, which created records like the ones in Figures 14.3 and 14.4. The Haskins researchers hoped to use the speech spectrograph to identify the acoustic signal that went with each phoneme.

However, much to their surprise, it turned out that there wasn't a pattern because the same phoneme could have different acoustic patterns in different contexts. The classic example of this is the example of coarticulation, illustrated in Figure 14.5, in which the /d/ sound in /di/ and /du/ have very different acoustic signals, even though the /d/ sounds the same in both cases. The di/du spectrograms are an example of the variability problem—the same phoneme can have different acoustic patterns in different contexts.

Having discovered that there is no one-to-one correspondence between acoustic signals and phonemes, the Haskins researchers shifted gears and turned their attention to explaining the basis of speech perception. To achieve this, they used the following reasoning: The acoustic signal can't stand for phonemes, because of the variability problem. So what property of speech is less variable? What property comes closer to a one-to-one correspondence with phonemes?

The answer to these questions was described in papers by Alvin Liberman and coworkers titled "A Motor Theory of Speech Perception" (1963) and "Perception of the Speech Code" (1967). The **motor theory of speech perception** proposed that motor commands are the property that avoids the variability problem because they have a one-to-one relationship to phonemes.

The Proposed Connection Between Production and Perception

According to motor theory, *hearing* a sound triggers motor processes in the listener associated with *producing* the sound. This connection between production and perception made sense to the Haskins researchers, because perceivers are also speakers, so they felt that it is natural that producing and perceiving would be related.

One of the problems with this theory, in the eyes of other researchers, was that it was unclear what or where the motor commands were that stood for each phoneme. In a later version of motor theory, it was stated that these motor commands are located in the brain (Liberman & Mattingly, 1989). But exactly where are these commands and what do they look like? The answer wasn't clear.

Motor theory stimulated a large number of experiments, some obtaining results that supported the theory, but many obtaining results that argued against it. It is difficult for motor theory to explain, for example, how people with brain damage that disables their speech motor system can still perceive speech (Lotto et al., 2009; Stasenko, 2013), or how young infants can understand speech before they have learned to speak (Eimas et al., 1987). Evidence such as this, plus the fact that the actual source of the motor information was never made clear, led many speech perception researchers to reject the idea that our perception of speech depends on the activation of motor mechanisms (Lane, 1965; Whalen, 2019).

The Proposal That "Speech Is Special"

Along with proposing the production-perception link, motor theory also proposed that speech perception is based on a special mechanism that is different from other auditory mechanisms. This conclusion was based on experiments studying a phenomenon called **categorical perception**, which occurs when stimuli that exist along a continuum are perceived as divided into discrete categories.

The Haskins researchers demonstrated categorical perception using a property of the speech stimulus called **voice onset time (VOT)**, the time delay between when a sound begins and when the vocal cords begin vibrating. We can illustrate this delay by comparing the spectrograms for the sounds /da/ and /ta/ in **Figure 14.7**. These spectrograms show that the time

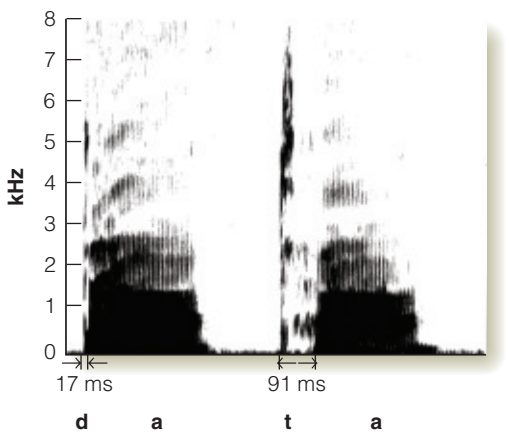

Figure 14.7 Spectrograms for /da/ and /ta/. The voice onset time—the time between the beginning of the sound and the onset of voicing—is indicated at the beginning of the spectrogram for each sound. (Spectrogram courtesy of Ron Cole)

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between the beginning of the sound and the beginning of the vocal cord vibrations (indicated by the presence of vertical stripes in the spectrogram) is 17 ms for /da/ and 91 ms for /ta/. Thus, /da/ has a short VOT, and /ta/ has a long VOT.

The Haskins researchers created sound stimuli in which the VOT was varied in small equal steps from short to long. When they varied VOT, using stimuli like the ones shown in Figure 14.7, and asked listeners to indicate what sound they heard, the listeners reported hearing only one or the other of the two phonemes, /da/ or /ta/, even though a large number of stimuli with different VOTs were presented.

This result is shown in **Figure 14.8a** (Eimas & Corbit, 1973). At short VOTs, listeners heard /da/, and they continued reporting this even when the VOT was increased. But when the VOT reached about 35 ms, their perception abruptly changed, so they heard /ta/ at VOTs above 40 ms. The phonetic boundary is the VOT at which perception changes from one category to another.

One key result of the categorical perception experiment was that even though the VOT was changed continuously across a wide range, the listeners had the experience of perceiving only two categories: /da/ on one side of the phonetic boundary and /ta/ on the other side. Another result was that when listeners were presented with two sounds separated by a VOT of, say, 25 ms that are on the same side of the phonetic boundary, such as stimuli with VOTs of 0 and 25 ms, the listener says they sound the same (**Figure 14.8b**). However, when we present two stimuli that are separated by the same difference in VOT but are on opposite sides of the phonetic boundary, such as stimuli with VOTs of 25 and 50 ms, the listener says they sound different. The fact that all stimuli on the same side of the phonetic boundary are perceived as the same category is an example of perceptual constancy.

You may remember perceptual constancy from our discussion of color and lightness constancy in Chapter 9. In color constancy, we perceive the color of objects as staying the same even when the illumination is changed. In lightness constancy, whites, grays, and blacks are perceived as staying the same shade under different illuminations (a white dog looks white under dim indoor illumination and intense outdoor sunlight). In the perceptual constancy of speech sounds, we identify sounds as the same phoneme, even as VOT is changed over a large range.

Liberman and coworkers' 1967 paper proposed that categorical perception provided evidence for a special speech decoder that is different than the mechanism involved in hearing non-speech sounds. However, other researchers rejected this idea when categorical perception was demonstrated for non-speech sounds (Cutting & Rosner, 1974), preverbal infants (Eimas et al., 1971), chinchillas (Kuhl & Miller, 1978), and budgerigars (parakeets) (Dooling et al., 1989).

Why was the motor theory important? One reason is that it attempted to deal with the main problem in understanding speech perception—the variable relationship between the

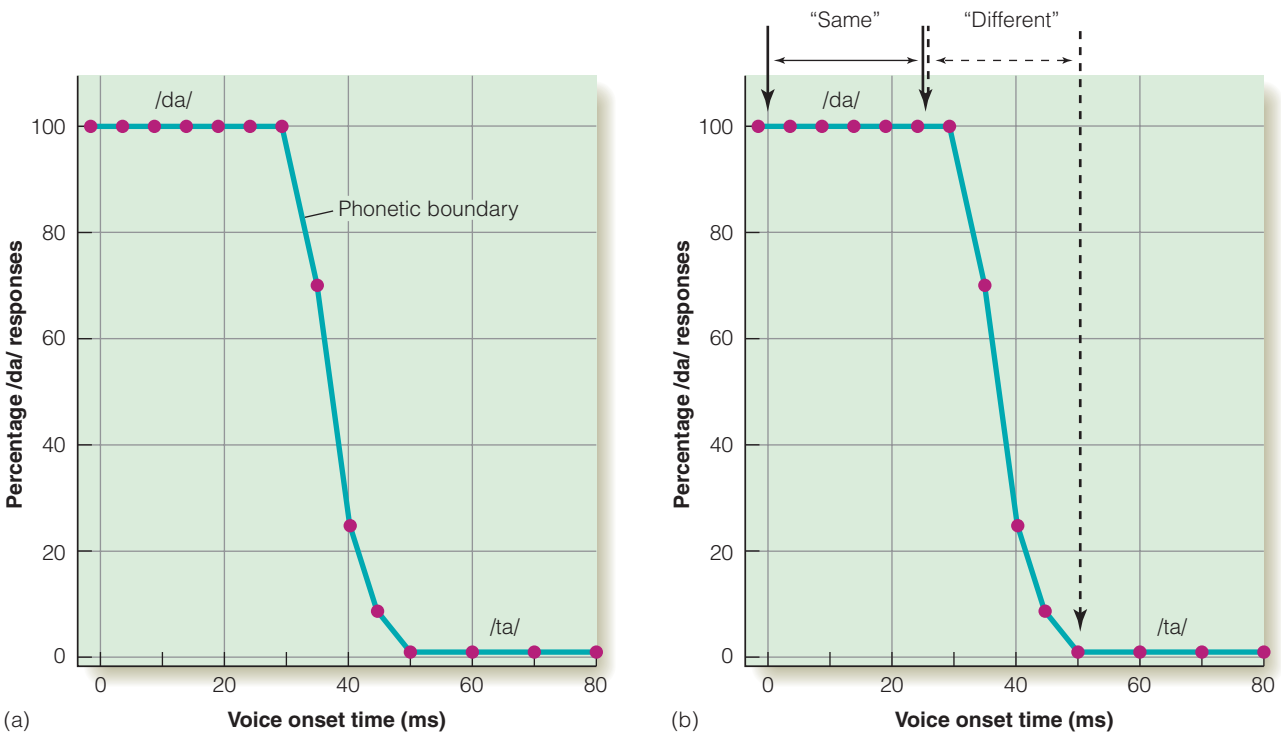

Figure 14.8 (a) The results of a categorical perception experiment indicating a phonetic boundary, with /da/ perceived for VOTs to the left and /ta/ perceived for VOTs to the right. (From Eimas & Corbit, 1973) (b) In the discrimination part of a categorical perception experiment, two stimuli are presented, and the listener indicates whether they are the same or different. The typical result is that two stimuli with VOTs on the same side of the phonetic boundary (VOT = 0 and 25 ms; solid arrows) are judged to be the same, whereas two stimuli on different sides of the phonetic boundary (VOT = 25 ms and 50 ms; dashed arrows) are judged to be different.

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acoustic signal and phonemes. While motor theory didn't solve the problem of variability, it influenced later researchers to study the problem, and also stimulated research on the connection between production and perception. As it turns out, although most researchers do not accept the idea that motor commands are the major mechanism responsible for speech perception, there is evidence for some connections between motor processes and speech perception, which we will consider in the next section.

Finally, what about categorical perception? While it didn't end up supporting the idea of a special speech mechanism, it is nonetheless an interesting and important phenomenon because it helps explain how we can perceive speech sounds that happen very quickly, reaching rates as high as 15–30 phonemes per second (Liberman et al., 1967). Categorical perception helps simplify things by transforming a long string of voice onset times into two categories. So the system doesn't have to register a particular sound's exact VOT; it just has to place the sound in a category that contains many VOTs.

This story of early speech perception research and theorizing is important because it ushered in the beginning of modern research on speech perception and stimulated a great deal of research, which identified a wide range of information that listeners take into account in perceiving speech. We will describe this information in the next section.

TEST YOURSELF 14.1

1. Describe the acoustic signal. Be sure you understand how speech sounds are represented on a speech spectrogram.
2. What are phonemes? Why is it not possible to describe speech as a string of phonemes?
3. What are two sources of variability that affect the relationship between the acoustic signals and the sounds we hear? Be sure you understand coarticulation.
4. Describe the motor theory of speech perception. What is the proposed connection between production and perception?
5. What is categorical perception? Be sure you understand how it is measured and why proponents of the motor theory thought it was important.
6. What is the present status of motor theory?

14.4 Information for Speech Perception

We've seen that the variability of the speech signal has made it difficult to determine exactly what information a listener uses in order to perceive speech. This situation is similar to the one we encountered for perceiving visual objects. Remember that the problem for vision was that an object's image on the retina is ambiguous (see page 92). The solution proposed by Hermann von Helmholtz involves a process called *unconscious inference*, in which we infer, based on whatever information is available, what object is most likely to have created a particular image on the retina (p. 107).

Many researchers have taken a similar approach to speech by proposing that listeners use multiple sources of information to perceive the ambiguous speech stimulus (Devlin & Aydelott, 2009; Skipper et al., 2017). One of the sources of information is motor processes.

Motor Processes

Although motor processes may not be the centerpiece of speech perception as proposed by motor theory, modern researchers have demonstrated some connections between motor processes and perceiving speech sounds.

Alessandro D'Ausilio and coworkers (2009) used the technique of *transcranial magnetic stimulation* (TMS) (see Method: Transcranial Magnetic Stimulation (TMS), page 185), to show that stimulation of motor areas associated with making specific sounds can aid in perception of these sounds. **Figure 14.9** shows the sites of TMS stimulation on the motor area of the cortex. Stimulation of the lip area resulted in faster responding to labial phonemes (/b/ and /p/) and stimulation of the tongue area resulted in faster responding to the dental phonemes (/t/ and /d/). Based on these results, D'Ausilio suggested that activity in the motor cortex can influence speech perception.

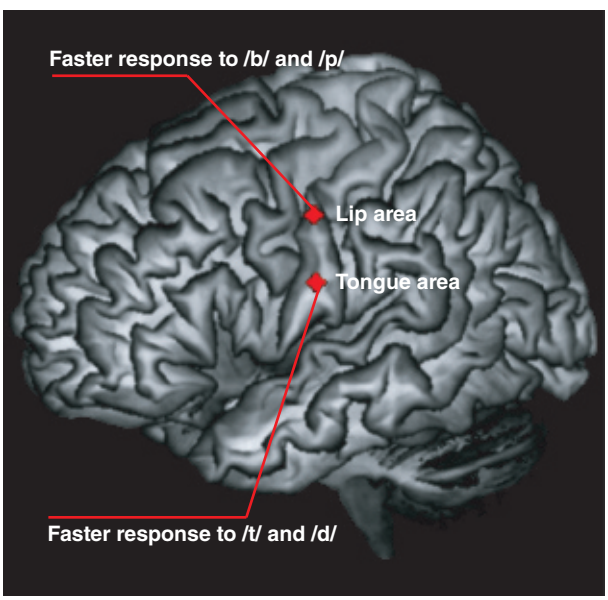

Figure 14.9 Sites of transcranial magnetic stimulation of the motor area for lips and tongue. Stimulation of the lip area increases the speed of responding to /b/ and /p/. Stimulation of the tongue area increases the speed of responding to /t/ and /d/. (From D'Ausilio et al., 2009)

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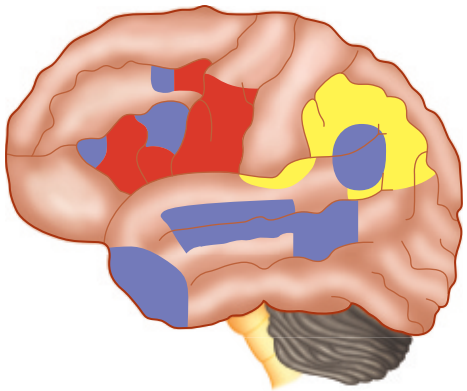

Figure 14.10 Left hemispheres of the cortex, showing areas activated by producing speech (red) and comprehending speech (yellow), and areas that respond to both production and comprehension (blue). (From Silbert et al., 2014)

The link between producing and perceiving speech has also been studied using fMRI. Lauren Silbert and coworkers (2014) measured the fMRI response to two 15-minute stories under two conditions: (1) when the person in the scanner was *telling the story* (production condition) and (2) when the person in the scanner was *listening to the story* (comprehension condition). **Figure 14.10** shows that Silbert found areas that responded when a person was producing speech (red areas) and when a person was comprehending speech (yellow areas). But she also found areas that responded both when speech was being produced *and* when it was being comprehended (blue areas).

Just because the same brain regions respond during both production and comprehension doesn't necessarily mean that they share processing mechanisms. It is possible that different kinds of processing could be going on within these regions for these two different tasks. But the possibility that production and comprehension share processing mechanisms is supported by Silbert's finding that the brain's response to production and comprehension was "coupled." That is, the time course of the neural responses to these two processes was similar.

Another argument for links between speech production and perception is based on the interconnectedness of different circuits in the brain. Mark Schomers and Freidman Pulvermüller (2016) use the diagrams in **Figure 14.11** to compare two theoretical positions regarding how the brain is involved in speech perception. The diagram on the left pictures the speech production and perception networks as separated. The diagram on the right pictures the two networks as connected and also being connected to the dorsal action network and the ventral vision network (see Chapter 4, page 80). They then present evidence in favor of the network-interaction model on the right.

The idea that motor processes are one source of information that is used to understand speech is still being researched, with some researchers assigning motor processes a small role in speech perception (Hickock, 2009; Stokes et al., 2019) and others assigning it a greater role (Schomers & Pulvermüller, 2016; Skipper et al., 2017; Wilson, 2009). Next, we will consider evidence that the face and movements of the lips provide information for speech perception.

The Face and Lip Movements

Another property of speech perception is that it is **multimodal**; that is, understanding speech can be influenced by information from senses such as vision and touch. One illustration of how speech perception can be influenced by visual information is shown in **Figure 14.12**. The woman seen in the monitor is saying /ba-ba/, but the woman's lip movements are those that would produce the sounds /fa-fa/. The listener therefore hears the sound as /fa-fa/ to match the lip movements he is *seeing*, even though the acoustic signal corresponds to /ba-ba/. (Note that when the listener closes his eyes, his perception is no longer influenced by what he is seeing and he hears /ba-ba/.)

This effect is called the **McGurk effect**, after Harry McGurk, who first described it along with John MacDonald

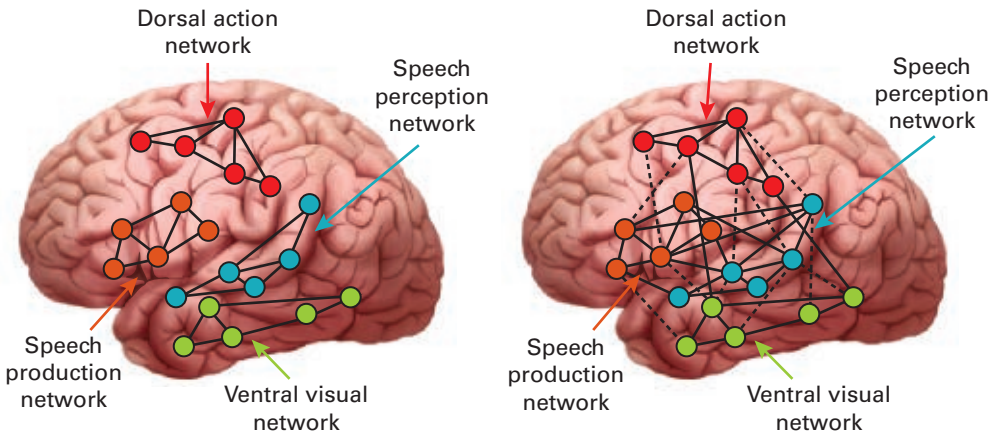

Figure 14.11 Two ways of thinking about the relation between speech production and perception. The diagram on the left pictures the networks serving speech production and perception as separated. The diagram on the right pictures the networks as connected and are also connected to the dorsal action network and ventral visual networks (see page 81). Schomers and Pulvermüller (2016) present evidence favoring the interconnected network diagram on the right.

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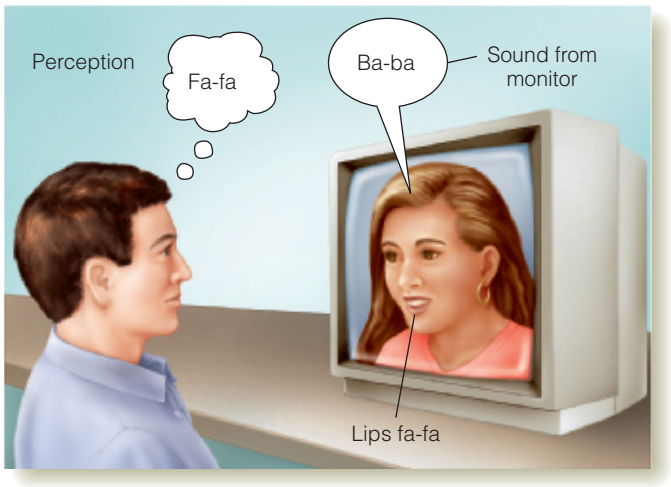

Figure 14.12 The McGurk effect. The women is saying /ba-ba/ but her lip movements correspond to /fa-fa/, so the listener reports hearing /fa-fa/.

(McGurk & MacDonald, 1976). It illustrates that although auditory information is the major source of information for speech perception, visual information can also exert a strong influence on what we hear (see "Something to Consider: Interactions Between Hearing and Vision" in Chapter 12, page 306). This influence of vision on speech perception is called **audiovisual speech perception**. The McGurk effect is one example of audiovisual speech perception. Another example is the way people routinely use information provided by a speaker's lip movements to help understand speech in a noisy environment (also see Sumby & Pollack, 1954).

The link between vision and speech has been shown to have a physiological basis. Gemma Calvert and coworkers (1997) used fMRI to measure brain activity as observers watched a silent videotape of a person making mouth movements for saying numbers. Observers silently repeated the numbers as they watched, so this task was similar to what people do when they read lips. In a control condition, observers watched a static face while silently repeating numbers. A comparison of the brain activity in these two conditions showed that watching the lips move activated an area in the auditory cortex that Calvert had shown in another experiment to be activated when people are perceiving speech. Calvert suggests that the fact that the same areas are activated for lipreading and speech perception is evidence for a neural mechanism behind the McGurk effect.

The link between speech perception and face perception was demonstrated in another way by Katharina von Kriegstein and coworkers (2005), who measured fMRI activation as listeners were carrying out a number of tasks involving sentences spoken by familiar speakers (people who also worked in the laboratory) and unfamiliar speakers (people they had never heard before).

Just listening to speech activated the superior temporal sulcus (STS; see Figure 5.42 page 111), an area that had been associated in previous studies with speech perception (Belin et al., 2000). But when listeners were asked to carry out a task that involved paying attention to the sounds of familiar voices, the fusiform face area (FFA) was also activated. In contrast, paying attention to the sounds of unfamiliar voices did not activate the FFA. Apparently, when people hear a voice that they associate with a specific person, this activates areas not only for perceiving speech but also for perceiving faces. The link between perceiving speech and perceiving faces, which has been demonstrated in both behavioral and physiological experiments, provides information that helps us deal with the variability of phonemes (for more on the link between observing someone speaking and perceiving speech, see Hall et al., 2005; McGettigan et al., 2012; van Wassenhove et al., 2005).

Knowledge of Language

A large amount of research has shown that it is easier to perceive phonemes that appear in a meaningful context. Philip Rubin and coworkers (1976), for example, presented a series of short words, such as *sin*, *bat*, and *leg*, or nonwords, such as *jum*, *baf*, and *teg*, and asked listeners to respond by pressing a key as rapidly as possible whenever they heard a sound that began with /b/. On average, participants took 631 ms to respond to the nonwords and 580 ms to respond to the real words. Thus, when a phoneme was at the beginning of a real word, it was identified about 8 percent faster than when it was at the beginning of a meaningless syllable.

The effect of meaning on the perception of phonemes was demonstrated in another way by Richard Warren (1970), who had participants listen to a recording of the sentence "The state governors met with their respective legislatures convening in the capital city." Warren replaced the first /s/ in "legislatures" with the sound of a cough and told his participants that they should indicate where in the sentence the cough occurred. None of the participants identified the correct position of the cough, and, even more significantly, none noticed that the /s/ in "legislatures" was missing. This effect, which Warren called the **phonemic restoration effect**, was experienced even by students and staff in the psychology department who knew that the /s/ was missing.

Warren not only demonstrated the phonemic restoration effect but also showed that it can be influenced by the meaning of words following the missing phoneme. For example, the last word of the phrase "There was time to *ave..." (where the * indicates the presence of a cough or some other sound) could be "shave," "save," "wave," or "rave," but participants heard the word "wave" when the remainder of the sentence had to do with saying good-bye to a departing friend.

Arthur Samuel (1990) also demonstrated top-down processing by showing that longer words increase the likelihood of the phonemic restoration effect. Apparently, participants used the additional context provided by the long word to help identify the masked phoneme. Further evidence for the importance of context is Samuel's finding that more restoration occurs for a real word such as *prOgress* (where the capital letter indicates the masked phoneme) than for a similar pseudoword such as *crOgress* (Samuel, 1990; also see Samuel, 1997, 2001, for more evidence that top-down processing is involved in phonemic restoration).

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The Meaning of Words in Sentences

It has been said that "all language begins with speech" (Chandler, 1950), but we can also say that perceiving speech is aided by language. One illustration of this is that when words are in a sentence, they can be read even when they are incomplete, as in the following demonstration.

DEMONSTRATION | Perceiving Degraded Sentences

Read the following sentences:

1. M*R* H*D * L*TTL* L*MB I*S FL**C* W*S WH*T* *S SN*W
2. TH* S*N *S N*T SH*N*NGT*D**
3. S*M* W**DS *R* EA*I*RT* U*D*R*T*N*T*A* *T*E*S

Your ability to read the sentences, even though half of the letters have been eliminated, was aided by your knowledge of English words, how words are strung together to form sentences, and perhaps in the first example, your familiarity with the nursery rhyme (Denes & Pinson, 1993).

A similar effect of meaningfulness also occurs for spoken words. A classic experiment by George Miller and Steven Isard (1963) demonstrated how meaningfulness makes it easier to perceive spoken words by showing that words are more intelligible when heard in the context of a grammatical sentence than when presented as items in a list of unconnected words. They demonstrated this by creating three kinds of stimuli: (1) normal grammatical sentences, such as *Gadgets simplify work around the house*; (2) anomalous sentences that follow the rules of grammar but make no sense, such as *Gadgets kill passengers from the eyes*; and (3) ungrammatical strings of words, such as *Between gadgets highways passengers the steal*.

Miller and Isard used a technique called **shadowing**, in which they presented these sentences to participants through earphones and asked them to repeat aloud what they were hearing. The participants reported normal sentences with an accuracy of 89 percent, but their accuracy fell to 79 percent for the anomalous sentences and 56 percent for the ungrammatical strings. The differences among the three types of stimuli became even greater when the listeners heard the stimuli in the presence of a background noise. For example, at a moderately high level of background noise, accuracy was 63 percent for the normal sentences, 22 percent for the anomalous sentences, and only 3 percent for the ungrammatical strings of words. These results tell us that when words are arranged in a meaningful pattern, we can perceive them more easily. But most people don't realize it is their knowledge of the nature of their language that helps them fill in sounds and words that might be difficult to hear. For example, our knowledge of permissible word structures tells us that ANT, TAN, and NAT are all permissible sequences of letters in English, but that TQN or NQT cannot be English words.

A similar effect of meaning on perception also occurs because our knowledge of the rules of grammar tells us that "There is no time to question" is a permissible English sentence, but "Question, no time there is" is not permissible or, at best, is extremely awkward (unless you are Yoda, who says this in *Star Wars, Episode III: Revenge of the Sith*). Because we mostly encounter meaningful words and grammatically correct sentences, we are continually using our knowledge of what is permissible in our language to help us understand what is being said. This becomes particularly important when listening under less than ideal conditions, such as in a noisy environment or when the speaker's voice quality or accent is difficult to understand, as we will discuss later in the chapter (see also Salasoo & Pisoni, 1985).

Another example of the effect of meaning on perception is that even though the acoustic signal for spoken sentences is continuous, with either no physical breaks in the signal or breaks that don't necessarily correspond to the breaks we perceive between words (**Figure 14.13**), we usually have little trouble perceiving individual words when conversing with another person. The perception of individual words in a conversation is called **speech segmentation**.

The fact that there are often no spaces between words becomes obvious when you listen to someone speaking a foreign language. To someone who is unfamiliar with that language, the words seem to speed by in an unbroken string. However, to a speaker of that language, the words seem separated, just as the words of your native language seem separated to you. We somehow solve the problem of speech segmentation and divide the continuous stream of the acoustic signal into a series of individual words.

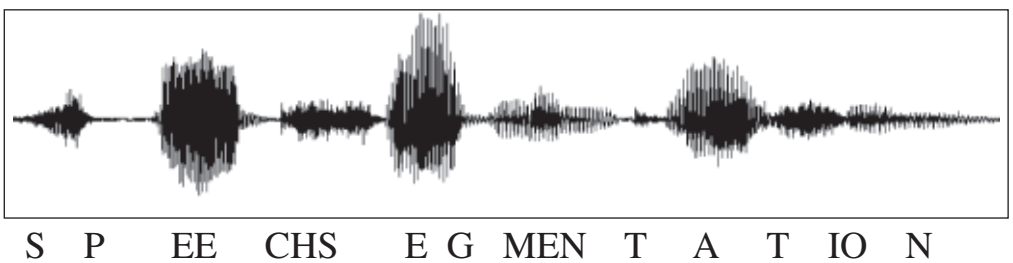

Figure 14.13 Sound energy for the words "speech segmentation." Notice that it is difficult to tell from this record where one word ends and the other begins. (Speech signal courtesy of Lisa Sanders)

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The fact that we can perceive individual words in conversational speech, even though there are few breaks in the speech signal, means that our perception of words is not based only on the energy stimulating the receptors. One thing that helps us tell when one word ends and another begins is knowledge of the meanings of words. The link between speech segmentation and meaning is illustrated in the following demonstration.

DEMONSTRATION | Organizing Strings of Sounds

Read the following words: *Anna Mary Candy Lights* out loud, speaking rapidly and ignoring the spaces between the words.

Now that you've read the words, what do they mean?

If you succeeded in creating the phrase "An American Delights" from the series of words, you did so by changing the perceptual organization of the sounds, and this change was achieved by your knowledge of the meaning of the sounds. Another example of how meaning and prior knowledge or experience are responsible for organizing sounds into words is provided by these two sentences:

Jamie's mother said, "Be a *big girl* and eat your vegetables."

The thing *Big Earl* loved most in the world was his car.

"Big girl" and "Big Earl" are both pronounced the same way, so hearing them differently depends on the overall meaning of the sentence in which these words appear. (Slight differences in stress may also play a role here.) This example is similar to the familiar "I scream, you scream, we all scream for ice cream" that many people learn as children. The sound stimuli for "I scream" and "ice cream" are identical, so the different organizations must be achieved by the meaning of the sentence in which these words appear.

While segmentation is aided by knowing the meanings of words and making use of the context in which these words occur, listeners use other information as well to achieve segmentation. As we learn a language, we learn that certain sounds are more likely to follow one another within a word, and other sounds are more likely to be separated by the space between two words.

Learning About Words in a Language

Consider the words *pretty baby*. In English it is likely that *pre* and *ty* will be in the same word (***pre-tty***) and that *ty* and *ba* will be separated by a space so will be in two different words (pre***tty ba***by). Thus, the space in the phrase *prettybaby* is most likely to be between *pretty* and *baby*.

Psychologists describe the way sounds follow one another in a language in terms of **transitional probabilities**—the chances that one sound will follow another sound. Every language has transitional probabilities for different sounds, and as we learn a language, we not only learn how to say and understand words and sentences, but we also learn about the transitional probabilities in that language. The process of learning about transitional probabilities and about other characteristics of language is called **statistical learning**. Research has shown that infants as young as 8 months of age are capable of statistical learning.

Jennifer Saffran and coworkers (1996) carried out an early experiment that demonstrated statistical learning in young infants. **Figure 14.14a** shows the design of this experiment. During the learning phase of the experiment, the infants heard strings of nonsense "words" such as *bidaku*, *padoti*, *golabu*, and *tupiro*, which were combined in random order to create 2 minutes of continuous sound. An example of part of a string created by combining these words is *bidaku**padoti**golabu**tupiro**padoti**bidaku*.... In this string, every other word is printed in boldface in order to help you pick out the words. However, when the infants heard these strings, all the words were pronounced with the same intonation, and there were no breaks between the words to indicate where one word ended and the next one began.

Because the words were presented in random order and with no spaces between them, the 2-minute string of words the infants heard sounds like a jumble of random sounds. However, there was information within the string of words in the form of transitional probabilities, which the infants could potentially use to determine which groups of sounds were words.

The transitional probabilities between two syllables that appeared *within* a word was always 1.0. For example, for the word *bidaku*, when /*bi*/ was presented, /*da*/ always followed it. Similarly, when /*da*/ was presented, /*ku*/ always followed it. In other words, these three sounds always occurred together and in the same order, to form the word *bidaku*. However, the transitional probabilities between the *end* of one word and the *beginning* of another was only 0.33. For example, there was a

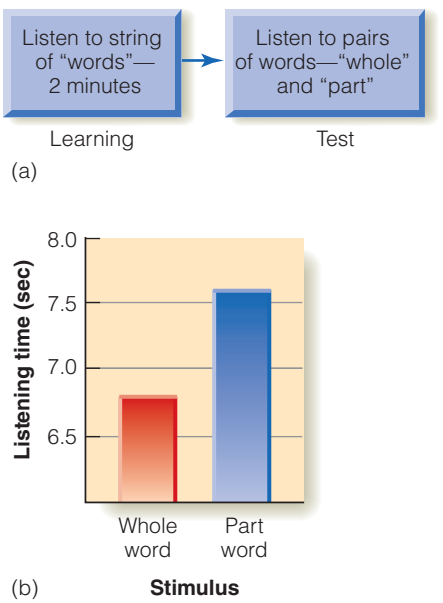

Figure 14.14 (a) Experimental design of the experiment by Saffran and coworkers (1996), in which infants listened to a continuous string of nonsense syllables and were then tested to see which sounds they perceived as belonging together. (b) The results, indicating that infants listened longer to the "part-word" stimuli.

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33 percent chance that the last sound, /*ku*/ from *bidaku*, would be followed by the first sound, /*pa*/, from *padoti*, a 33 percent chance that it would be followed by /*tu*/ from *tupiro*, and a 33 percent chance it would be followed by /*go*/ from *golabu*.

If Saffran's infants were sensitive to transitional probabilities, they would perceive stimuli like *bidaku* or *padoti* as words, because the three syllables in these words are linked by transitional probabilities of 1.0. In contrast, stimuli like *tibida* (the end of *padoti* plus the beginning of *bidaku*) would not be perceived as words, because the transitional probabilities were much smaller.

To determine whether the infants did, in fact, perceive stimuli like *bidaku* and *padoti* as words, the infants were tested by being presented with pairs of three-syllable stimuli. One of the stimuli was a "word" that had been presented before, such as *padoti*. This was the "whole-word" test stimulus. The other stimulus was created from the end of one word and the beginning of another, such as *tibida*. This was the "part-word" test stimulus.

The prediction was that the infants would choose to listen to the part-word test stimuli longer than to the whole-word stimuli. This prediction was based on previous research that showed that infants tend to lose interest in stimuli that are repeated, and so become familiar, but pay more attention to novel stimuli that they haven't experienced before (see habituation procedure, page 225). Thus, if the infants perceived the whole-word stimuli as words that had been repeated over and over during the 2-minute learning session, they would pay less attention to these familiar stimuli than to the more novel part-word stimuli that they did not perceive as being words.

Saffran measured how long the infants listened to each sound by presenting a blinking light near the speaker where the sound was coming from. When the light attracted the infant's attention, the sound began, and it continued until the infant looked away. Thus, the infants controlled how long they heard each sound by how long they looked at the light.

Figure 14.14b shows that the infants did, as predicted, listen longer to the part-word stimuli. These results are impressive, especially because the infants had never heard the words before, they heard no pauses between words, and they had only listened to the strings of words for 2 minutes. From results such as these, we can conclude that the ability to use transitional probabilities to segment sounds into words begins at an early age.

TEST YOURSELF 14.2

1. How have speech researchers been guided by Helmholtz's theory of unconscious inference?
2. How has transcranial magnetic stimulation (D'Ausilo experiment) and fMRI (Silbert experiment) been used to demonstrate a connection between speech production and perception?
3. What does measuring networks in the brain indicate about the possible link between production and perception?
4. What is the McGurk effect, and what does it illustrate about how speech perception can be influenced by visual information? What physiological evidence demonstrates a link between visual processing and speech perception?
5. Describe evidence that shows how perceiving phonemes is influenced by the context in which they appear. Describe the phonemic restoration effect and the evidence for both bottom-up and top-down processing in creating this effect.
6. What is the evidence that meaning can influence word perception?
7. What mechanisms help us perceive breaks between words?
8. Describe the Saffran experiment and the basic principle behind statistical learning.

14.5 Speech Perception in Difficult Circumstances

One thing you should be convinced of by now is that although the starting point for perceiving speech is the incoming acoustic signal, listeners also use top-down processing, involving their knowledge of meaning and the properties of language, to perceive speech. This additional information helps listeners deal with the variability of speech produced by different speakers. But in our everyday environment we have to deal with more than just different ways of speaking. We also have to deal with background noise, poor room acoustics, and smartphones under poor reception conditions, all of which prevent a clear acoustic signal from reaching our ears.

How well can we understand speech heard under adverse conditions? Research designed to answer this question has shown that listeners can adapt to adverse conditions by using top-down processing to "decode" the degraded acoustic signal. Matthew Davis and coworkers (2005) tested participants to determine their ability to perceive speech distorted by a process called *noise vocoding*. **Noise-vocoded speech** is created by dividing the speech signal up into different frequency bands and then adding noise to each band. This process transforms the spectrogram of the original speech stimulus on the left in **Figure 14.15** into the noisy spectrogram on the right. The loss of detail in the frequency representation of the noise-vocoded signal transforms clear speech into a harsh noisy whisper.

Participants in Davis's experiment listened to a vocoded sentence and then wrote down as much of the sentence as they could. This was repeated for a total of 30 sentences. **Figure 14.16** shows the average proportion of words reported correctly by six participants for each of the 30 sentences. Notice that performance was near zero for the first three sentences, and then increases, until by the 30th sentence, participants are reporting half or more of the words. (The variability occurs because some vocoded sentences are more difficult to hear than others.) The increase in performance shown in Figure 14.16 is

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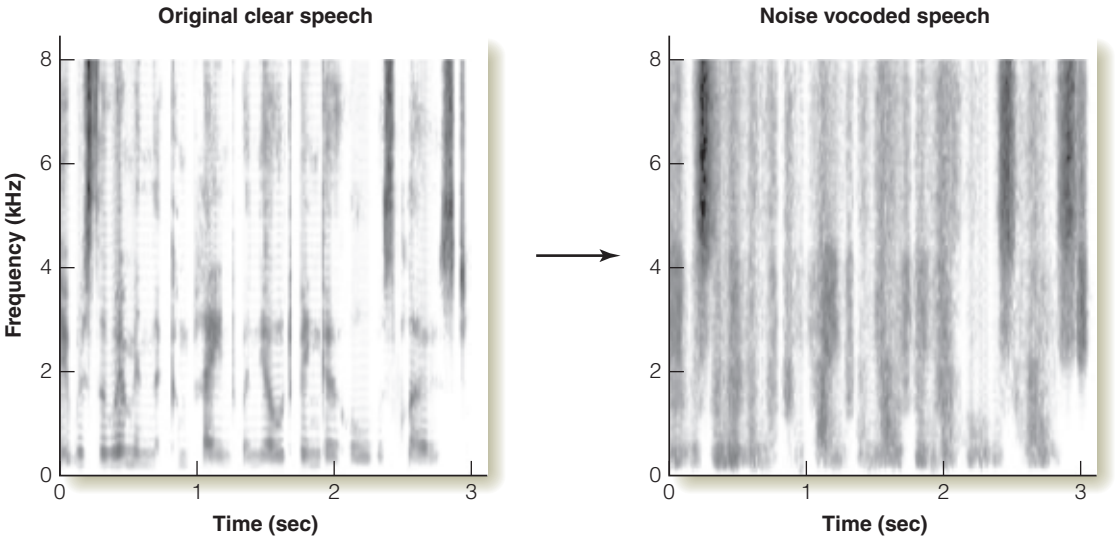

Figure 14.15 How the speech signal was changed for the Davis et al. (2005) noise vocoding experiment. The spectrogram of the original speech stimulus is on the left, and the noise-vocoded version is on the right. See text for details.

important because all the participants were doing is listening to one sentence after the other.

In another experiment, Davis's participants first listened to a degraded sentence and wrote down what they heard, as before, and then heard a clear, undistorted version of the sentence, followed by the distorted sentence again (hear degraded sentence → hear clear sentence → hear degraded sentence again). Participants reported that when they listened to the second presentation of the degraded sentence, they heard some words they hadn't heard the first time. Davis calls this ability to hear previously unintelligible words the "pop-out" effect.

The pop-out effect shows that higher-level information such as listeners' knowledge can improve speech perception. But this result becomes even more interesting when we consider that after experiencing the pop-out effect participants became better at understanding *other* degraded sentences that they were hearing for the first time. Even more interesting, the pop-out effect and later improvement in performance also occurred in a group of participants who *read* the sentence after hearing the degraded version (hear degraded sentence → read written sentence → hear degraded sentence again). What this means is that it wasn't listening to the clear sound that was important, but knowing the *content* (the speech sounds and words) of what they were hearing that helped with learning. Thus, this experiment provides another demonstration of how listeners can use information in addition to the acoustic signal to understand speech.

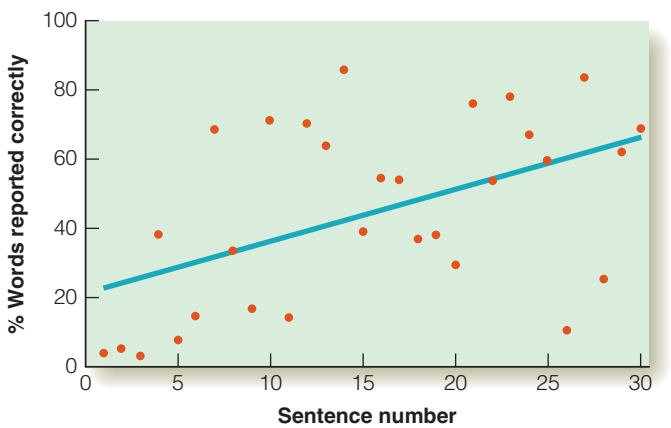

Figure 14.16 Perception of noise-vocoded words correctly identified for a series of 30 different sentences. Each data point is the average performance for the six subjects in Davis and coworkers' (2005) experiment.

What information can listeners pick up from degraded sentences? One possibility is the temporal pattern—the timing or rhythm of the speech. Robert Shannon and coworkers (1995) used noise-vocoded speech to demonstrate the importance of these slow temporal fluctuations. They showed that when most of the pitch information was eliminated from a speech signal, listeners were still able to recognize speech by focusing on temporal cues such as the rhythm of the sentence.

You can get a feel for the information carried by temporal cues by imagining what speech sounds like when you press your ears to a door and hear only muffled voices. Although hearing-through-the-door speech is difficult to understand, there is information in the rhythm of speaking that can lead to understanding. Much of this information comes from your knowledge of language, learned through years of experience.

One example of learning from experience is the learning of statistical regularities we discussed in connection with Saffran's infant experiments on page 346. We also discussed the idea of learning from experience in Chapter 5, when we described how visual perception is aided by our knowledge of regularities in the environment (p. 105). Remember the "multiple personalities of a blob" experiment in which perception of a blob-like shape depended on the type of scene in which it appeared (also see Figure 5.37 and see page 323 for a similar

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discussion related to music perception). Demonstrations such as this illustrate how knowledge of what usually happens in the visual environment influences what we see. Similarly, our knowledge of how certain speech sounds usually follow one another can help us learn to perceive words in sentences, even if the individual sounds are distorted.

The ability to determine what is being said, even when sounds are distorted, is something you may have experienced if you have ever listened to someone speaking with a foreign accent that was difficult to understand at first but became easier to understand as you continued to listen. If this has happened to you, it is likely that you were trying to understand what the person were saying—the overall meaning—without focusing on the sounds of individual words. But eventually, listening to determine the overall message results in an increased ability to understand individual words, which in turn makes it easier to understand the overall message. Clearly, transforming "sound" to "meaningful speech" involves a combination of bottom-up processing, based on the incoming acoustic signal, and top-down processing, based on knowledge of meanings and the nature of speech sounds.

14.6 Speech Perception and the Brain

Investigation of the physiological basis for speech perception stretches back to at least the 19th century, but considerable progress has been made recently in understanding the physiological foundations of speech perception and spoken word recognition. Let's begin with the classic observations of Paul Broca (1824–1880) and Carl Wernicke (1848–1905), who showed that damage to specific areas of the brain causes language problems, called **aphasias** (**Figure 14.17**). When Broca tested patients who had suffered strokes that damaged their frontal lobe, in an area that came to be called **Broca's area**, he found that their speech was slow and labored and often had jumbled sentence structure. (See Chapter 2, page 31, and Chapter 13, page 327 for more on Broca.) Here is an example of the speech of a modern patient, who is attempting to describe when he had his stroke, which occurred when he was in a hot tub.

> Alright. ... Uh... stroke and un. ... I... huh tawanna guy. ... H... h... hot tub and. ... And the. ... Two days when uh. ... Hos... uh. ... Huh hospital and uh... amet... am... ambulance. (Dick et al., 2001, p. 760)

Patients with this problem—slow, labored, ungrammatical speech caused by damage to Broca's area, are diagnosed as having **Broca's aphasia**. Later research showed that patients with Broca's aphasia not only have difficulty forming complete sentences, they also have difficulty understanding some types of sentences. Consider, for example, the following two sentences:

> The apple was eaten by the girl.
> The boy was pushed by the girl.

Patients with Broca's aphasia have no trouble understanding the first sentence but have difficulty with the second sentence. The problem they have with the second sentence is deciding whether the girl pushed the boy or the boy pushed the girl. While you may think it is obvious that the girl pushed the boy, patients with Broca's aphasia have difficulty processing connecting words such as "was" and "by," and this makes it difficult to determine who was pushed. (Notice what happens to the sentence when these two words are omitted.) You can see, however, that the first sentence cannot be interpreted in two ways. It is clear that the girl ate the apple, because it is not possible, outside of an unlikely science fiction scenario, for the apple to eat the girl (Dick et al., 2001; Novick et al., 2005). Taking into account the problems in both producing and understanding speech experienced by Broca's patients, modern researchers have concluded that damage to Broca's area in the frontal lobe causes problems in processing the structure of sentences.

The patients studied by Wernicke, who had damage to an area in their temporal lobe that came to be called **Wernicke's area**, produced speech that was fluent and grammatically correct but tended to be incoherent. Here is a modern example of the speech of a patient with **Wernicke's aphasia**.

> It just suddenly had a feffort and all the feffort had gone with it. It even stepped my horn. They took them from earth you know. They make my favorite nine to severed and now I'm a been habed by the uh stam of fortment of my annulment which is now forever. (Dick et al., 2001, p. 761)

Patients such as this not only produce meaningless speech but are unable to understand speech and writing. While patients with Broca's aphasia have trouble understanding sentences in which meaning depends on word order, as in "The boy was pushed by the girl," Wernicke's patients have more widespread difficulties in understanding and would be unable to understand "The apple was eaten by the girl" as well. In the most extreme form of Wernicke's aphasia, the person has

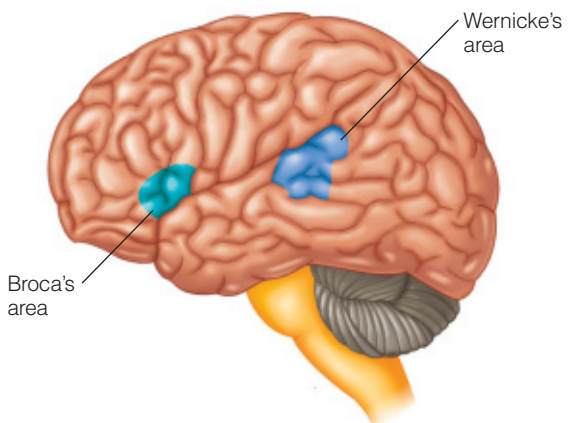

Figure 14.17 Broca's and Wernicke's areas. Broca's area is in the frontal lobe and Wernicke's is in the temporal lobe.

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a condition called **word deafness**, in which he or she cannot recognize words, even though the ability to hear pure tones remains intact (Kolb & Whishaw, 2003).

Modern research on speech and the brain has moved away from focusing on Broca's and Wernicke's areas to consider how speech perception involves multiple areas of the brain, some of which are specialized for specific speech functions. For example, we saw in Chapter 2 that Pascal Belin and coworkers (2000) used fMRI to locate a "voice area" in the human superior temporal sulcus (STS; see Figure 2.17) that is activated more by human voices than by other sounds, and Catherine Perrodin and coworkers (2011) recorded from neurons in the monkey's temporal lobe that they called **voice cells** because they responded more strongly to recordings of monkey calls than to calls of other animals or to "nonvoice" sounds.

The "voice area" and "voice cells" are located in the temporal lobe, which is part of the *what* processing stream for hearing that we described in Chapter 12 (see Figure 12.12, page 299). In describing the cortical organization for hearing in Chapter 12, we saw that the *what* pathway is involved in identifying sounds and the *where* pathway is involved in locating sounds. Piggybacking on this dual-stream idea for hearing, researchers have proposed a **dual-stream model of speech perception**. One version of this model is shown in **Figure 14.18**. The ventral stream supports speech comprehension and the dorsal stream may be involved in linking the acoustic signal to the movements used to produce speech (Hickock & Poeppel, 2015; Rauschecker, 2011).

In addition to considering the possible functions of the ventral and dorsal streams, other research has looked at how phonemes are represented in the brain. Nima Mesgarani and coworkers (2014) took advantage of the "standard procedure" for brain surgery for epilepsy, which involves using electrodes placed on the brain to determine the functional layout of a particular person's brain. **Figure 14.19a** shows the locations of the electrodes on the temporal lobe. Each dot is an electrode; the darker colored dots indicate locations at which neurons responded most strongly to speech when participants listened to 500 sentences spoken by 400 different people.

Each column in **Figure 14.19b** shows the results for a single electrode. Red and dark red indicate the neural response for the first 0.4 seconds after the onset of each phoneme, listed on the left. Each of these electrodes records responses to a group of phonemes. For example, electrode 1 responds to consonants like /d/, /b/, /g/, /k/, and /t/, and electrode 3 responded to vowels like /a/ and /ae/.

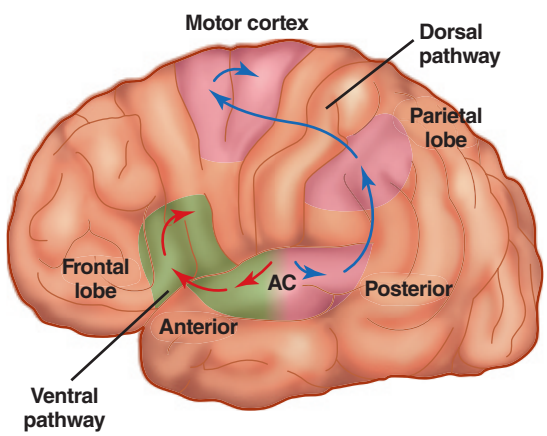

Figure 14.18 Human cortex showing the ventral pathway (red arrows) that is responsible for recognizing speech and the dorsal pathway (blue arrows) that links the acoustic signal and motor movements. AC = auditory cortex. The ventral pathway sends signals from the anterior auditory area to the frontal cortex. The dorsal pathway sends signals from the posterior auditory area to the parietal lobe and motor areas. (Adapted from Rauschecker, 2011)

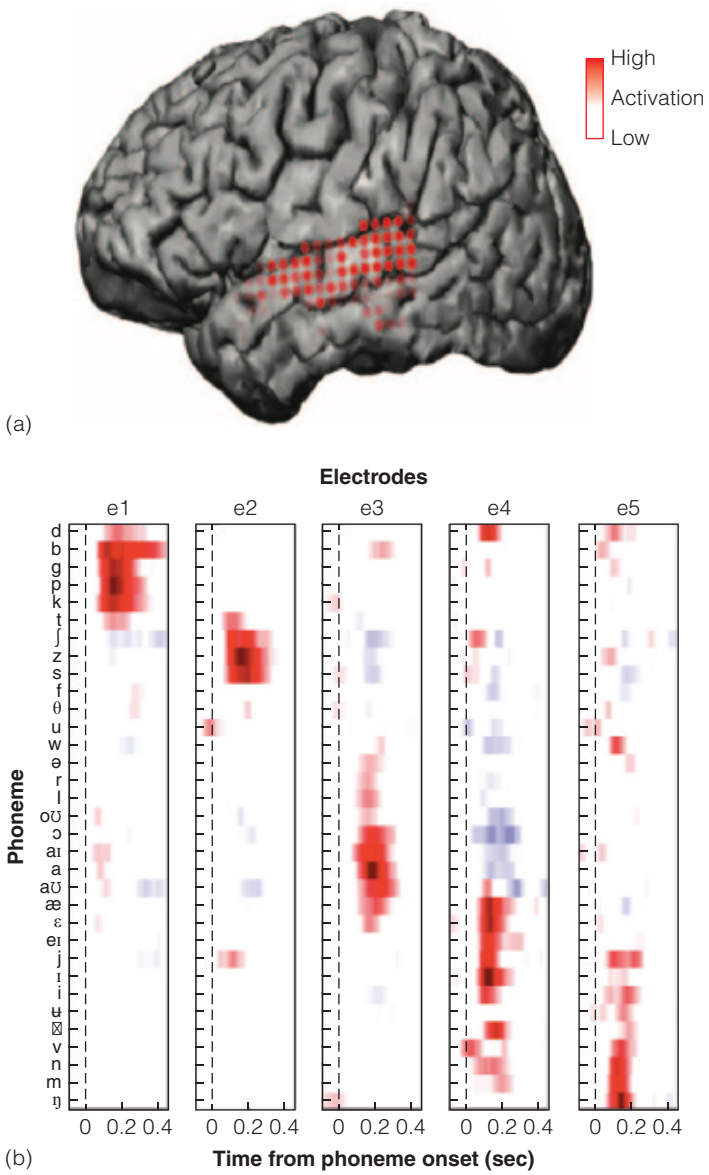

Figure 14.19 (a) The red dots indicate electrode placements on the temporal lobe for Mesgarani and coworkers' (2014) experiment. Darker dots indicate larger responses to speech sounds. (b) Average neural responses to the phonemes on the left, showing activity in red for 5 electrodes during the first 0.4 seconds after presentation of the phonemes.

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While Mesgarani and coworkers observed electrode responses corresponding to single phonemes, they also found responses corresponding to **phonetic features**, like *manner of articulation*, which describes how the articulators interact while making a speech sound, and *place of articulation*, which describes the location of articulation (p. 337). Mesgarani and coworkers found electrodes that were linked to specific phonetic features. For example, one electrode picked up responses to sounds that involved place of articulation in the back of the mouth, such as /g/, and another responded to sounds associated with places near the front, such as /b/.

Thus, neural responses can be linked both to phonemes, which specify specific sounds, and to specific features, which are related to the way these sounds are produced. If we consider the response to a particular phoneme or feature across all of the electrodes, we find that each phoneme or feature causes a pattern of activity across these electrodes. The neural code for phonemes and phonetic features therefore corresponds to population coding, which was described in Chapter 2 (see Figure 2.13, page 30).

What is important about studies such as this one is that they go beyond just identifying where speech is processed in the cortex. These studies, and many others, have provided information about how basic units of speech such as phonemes and the phonetic features associated with these phonemes are represented by patterns of neural responding.

SOMETHING TO CONSIDER:

Cochlear Implants

Our ability to hear speech depends, of course, on both the brain, which we have just been discussing, and on the hair cells inside the cochlea, which, as we saw in Chapter 11, generate the electrical signals that are sent to the brain. Damage to the hair cells causes **sensorimotor hearing loss**, which affects the ability to hear and perceive speech. If hearing is not completely lost, hearing can be partially restored by hearing aids, which amplify the sound that remains. However, if hearing loss is extreme or even complete, hearing aids can't help.

Prior to 1957, people with severe sensorimotor hearing loss were told that nothing could be done for their condition. But in 1957, Andre Djourno and Charles Eyries succeeded in eliciting sound sensations by stimulating a person's hair cells in the cochlea with an electrode placed in the inner ear. This was the first **cochlear implant** (CI). Later work created multielectrode CIs, with modern CIs having 12 to 22 electrodes. There are now more than half a million people who have been surgically fitted with cochlear implants (Svirsky, 2017).

The basic principle behind CIs is shown in **Figure 14.20**. The cochlear implant consists of (1) a microphone that receives sound signals from the environment; (2) a sound processor that divides the sound received by the microphone into a number of frequency bands; (3) a transmitter that sends these signals to (4) an array of 12–22 electrodes that are implanted along the length of the cochlea. These electrodes stimulate the cochlea at different places along its length, depending on the intensities of the frequencies in the stimuli received by the microphone. This stimulation activates auditory nerve fibers along the cochlea, which send signals toward the brain.

The placement of the electrodes is based on the topographic layout of the cochlea described by von Bekesy (p. 276), in which activation of hair cells near the base of the cochlea is associated with high frequencies, and activation near the apex is associated with low frequencies (see Figure 11.24, page 278).

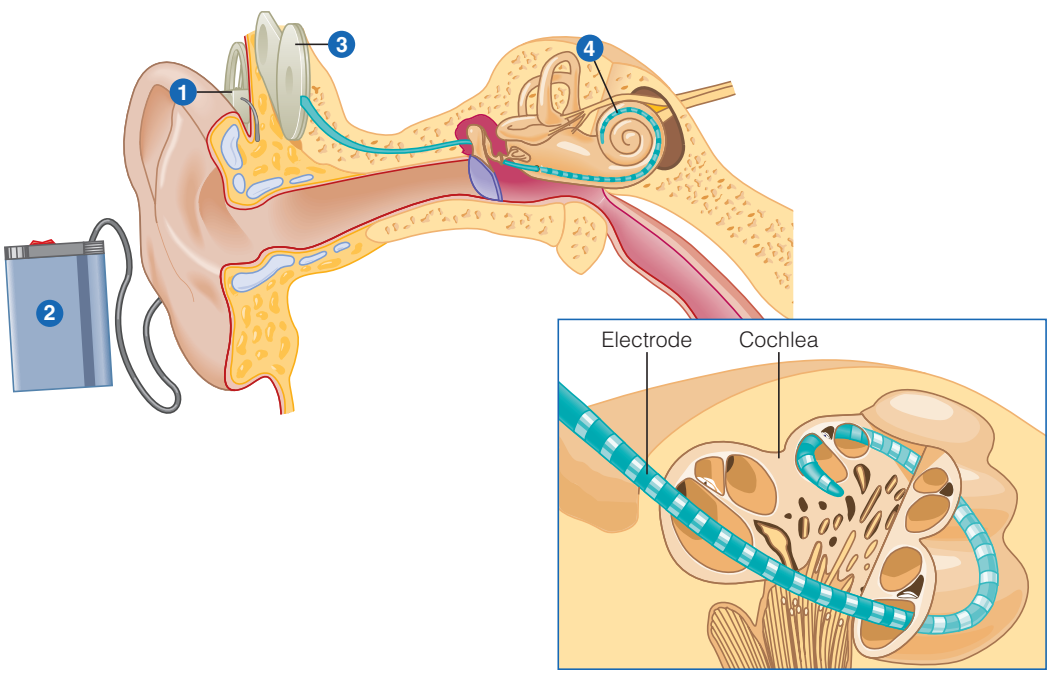

Figure 14.20 Cochlear implant. See text for details.

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Figure 14.21a shows a speech spectrogram for the word *Choice*. **Figure 14.21b** shows the pattern of electrical pulses delivered by the cochlear implant electrodes in response to the same word. Notice that "frequency" on the vertical axis of the spectrogram is replaced by "electrode number" on the vertical axis of the CI stimulation record.

There are two noteworthy things about the CI stimulation record. First, there is a correspondence between the spectrogram and the CI record. The high frequency stimulus between 3,500 and 5,000 Hz recorded on the spectrogram, which corresponds to the sound [Ch], is signaled by responses in electrodes 13–22. Also, frequencies below 3,000 that occur between 0.55 and 0.8 seconds on the spectrogram, which corresponds to the sound [oice], are signaled by responses in electrodes 1–11. This correspondence between the signal indicated by the spectrogram and the hair cells activated by the CI is what results in perception of a sound corresponding to *Choice*.

However, notice that the harmonics between 0.55 and 0.8 seconds in the spectrogram are blurred together in the CI signal. Thus, there is a correspondence between the audio signal indicated by the spectrogram and the CI signal, but it isn't perfect. One reason for this lack of complete correspondence is that the CI electrodes are separated from the hair cells by a wall of bone, which spreads the stimulation. Thus, a particular CI electrode stimulates many neurons, which causes the stimulation created by neighboring electrodes to overlap.

Because of these distortions, what a person with a CI hears is not the same as normal hearing. For example, people who had experienced some hearing before receiving their CI describe what they hear as a radio out of tune, Minnie Mouse, Donald Duck, or (less frequently) Darth Vader. Luckily, because the brain is plastic it can adapt to distorted input, so while a person's spouse might initially sound like a chipmunk, the quality and understandability of her voice typically improves over a period of weeks or months (Svirsky, 2017).

In clinical practice there is a great deal of variability between people who have received CIs, so one person might be able to perceive 100 percent of the words in sentences, and might even be able to use a telephone, while another person perceives nothing (Macherey & Carlyon, 2014). In one evaluation, people with some preoperative hearing were tested on their ability to perceive words in sentences (Parkinson et al., 2002). Their preoperative score was 11 percent correct, and postoperative, 78 percent correct. However, adding background noise made identifying words more difficult, and CI users often report that music sounds distorted or "non-musical" (Svirsky, 2017).

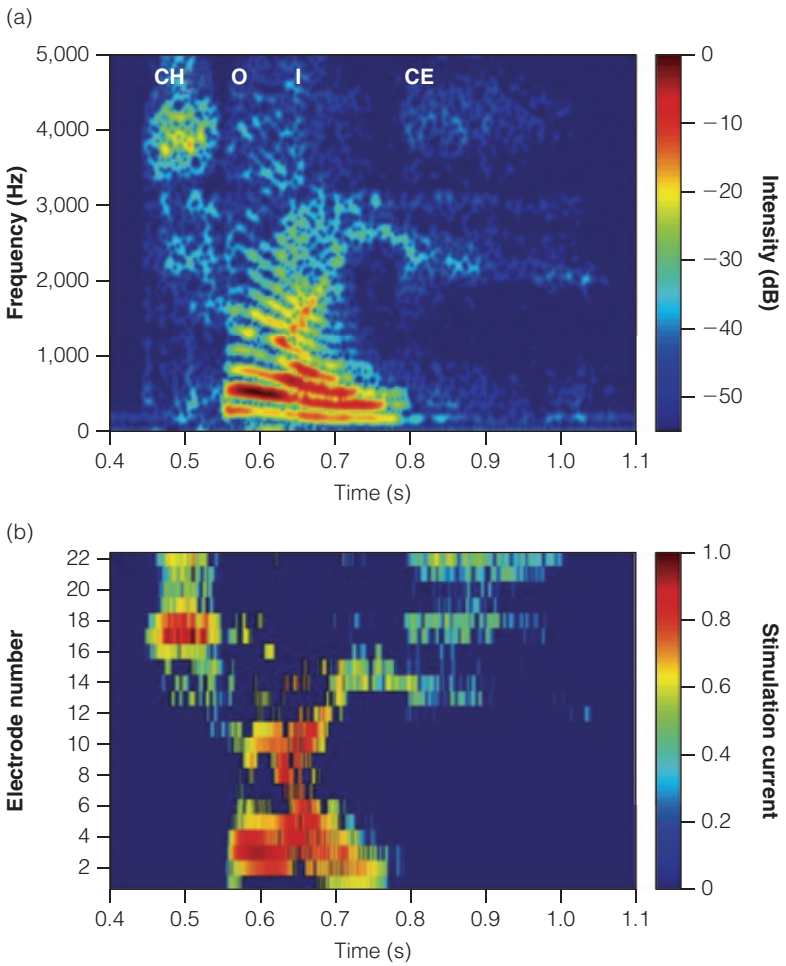

Figure 14.21 (a) Spectrogram created in response to the spoken word "choice." (b) Pattern of electrically stimulated pulses delivered to electrodes of a cochlear implant in response to the same word. Notice that the overall pattern of the O I record in (b) matches the spectrogram in (a), but that details of the spectrogram, such as the harmonic bands between 0.55 and 0.80 seconds, are missing. (Svirsky, 2017)

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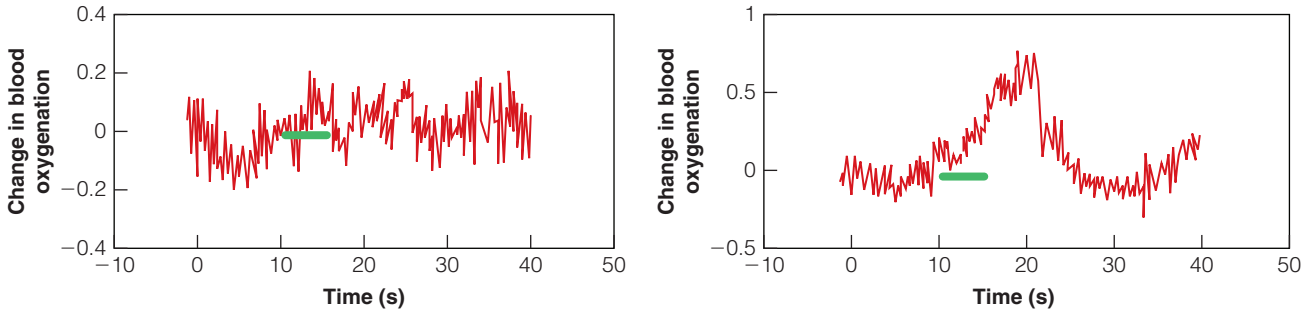

Figure 14.22 (a) The red record indicates blood oxygenation (which indicates neural activity), measured from the auditory cortex in a deaf child in response to auditory stimulation (green line), delivered before activation of the child's cochlear implant. Note that there is no response to the stimulation. (b) The record in response to auditory stimulation delivered after activation of the cochlear implant. (From Bortfeld, 2019)

An extremely important application of CI is its use in children, especially those who are born deaf. Using a special technique to measure brain activity in infants, Heather Bortfeld (2019) showed that there was no auditory cortex response in an infant before installing the CI, but a response did appear after the CI was installed (**Figure 14.22**).

One key to a successful outcome for children is to implant the CI at an early age. One study showed that if the CI is implanted by near the first birthday, children's speech and language skills can be near normal by the age of 4 1/2 and another study found that 75 percent of grade school children with implants were in mainstream education (Geers & Nicholas, 2013; Sharma et al., 2020). Because of results such as these, installing of CI is now standard clinical procedure for children who are born deaf (Machery & Carlyon, 2014). This early implantation is possible because the human cochlea is near adult size at birth, so children don't outgrow their electrode array.

The development of CI is an example of how basic research, which helps us understand the workings of a sensory system—like Bekesy's mapping of frequency along the cochlea—can have meaningful practical applications. In this case, CIs transform a world of silence into one in which speech can be heard and understood, which, in turn, leads to being able to use speech to communicate with others.

DEVELOPMENTAL DIMENSION Infant-Directed Speech

In the Developmental Dimension in Chapter 11, we saw that newborns can hear (although not as well as adults), and, because they can hear in the womb, newborns can recognize their mother's voice (DeCasper & Fifer, 1980). But perceiving and understanding speech goes beyond simply "hearing," because the sounds that newborns experience need to be transformed into words and then meaningful speech.

So how does a newborn negotiate the journey from hearing sounds to understanding someone talking? One thing that helps is that infants between 1 and 4 months of age can discriminate between different consonant sounds such as /ba/ and /ga/ or /ma/ and /na/ (Eimas et al., 1971), and between different vowel sounds such as /a/ and /i/, as in *had* versus *hid* (Trehub, 1973).

But speech perception involves more than discriminating between phonemes. It also involves learning both isolated words and words as they speed by within phrases or sentences, and also being able to understand the thoughts transmitted by strings of words.

The key to achieving this learning is to have a teacher. Often the primary teacher is the mother, but the father and others usually participate as well. This teaching occurs as the infant listens to people talk, but most importantly, as people talk directly to the infant, which brings us to the title of this section: Infant-directed speech.

Infant-directed speech (IDS), which is also called "motherese" (or more recently, "parentese,"), or "baby talk," has special characteristics that both attract an infant's attention and make it easier for the infant to recognize individual words. The characteristics of IDS that make it different than **adult-directed speech** (ADS) are: (1) higher in pitch, (2) larger range of pitches, (3) slower, (4) words are more separated, or totally isolated, and (5) words are often repeated. In addition, IDS often transmits positive affect.

Research has shown that the higher pitch and pitch range, and the positive affect help capture the infant's attention, so from birth through at least 14 months, infants prefer to listen to IDS compared to ADS (Fernald & Kuhl, 1987;

Continued

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McRoberts et al., 2009; Soderstrom, 2007). The larger range of pitches for IDS is pictured in the IDS "vowel triangle" shown in **Figure 14.23**. When the first and second formants of the IDS sounds /i/ as in *see*, /a/ as in *saw*, and /u/ as in *sue* are plotted, they create a larger triangle than do the same ADS sounds, and this larger range makes it easier to tell the difference between the sounds (Golinkoff et al., 2015; Kuhl et al., 1997).

The greater separation between sounds and words helps infants distinguish individual words, and another feature of IDS—saying key words at the end of a phrase—helps highlight these words. For example, saying "Can you see the doggie?" highlights "doggie" more than "The doggie is eating a bone," so "doggie" in the last position is more likely to be remembered (Liang, 2016). Saying words in isolation also helps, so a substantial proportion of the infant's first 30 to 50 words have typically been spoken in isolation by the mother. Examples are "bye bye," and "mommy" (Brendt & Siskind, 2001).

When parents are talking to children their goals may include "making a social connection," "being affectionate," and "making a connection between words and things." But whatever the goals, talking is always an opportunity for teaching. These teaching opportunities vary a lot from child to child, with the average child hearing 20,000 to 38,000 words a day, but the range being from 2,000 to 50,000 words a day (Hart & Risley, 1995; Shneidman et al., 2013; Weisleder & Fernald, 2013).

This range of words experienced by different children is important because there is a correlation between the number of words heard early in development, and later outcomes such as size of the vocabulary, learning to read, and achievement in school (Montag et al., 2018; Rowe, 2012). So talking to infants is good, and it's even better if they are paying attention, which is enhanced by IDS.

Finally, let's return to our earlier discussion of cochlear implants (CI) in children, in which we noted that it is important to install CIs early, so the infant can begin learning how to perceive speech and understand language. The importance of IDS is magnified in infants with CI because these infants typically show reduced attention to speech, compared to normal-hearing infants (Horn et al., 2007). In a study that measured the degree to which infants with CIs responded to IDS, Yuayan Wang and coworkers (2017) found that IDS increased these infants' attention to speech and words and was associated with better language comprehension. Infant-directed speech, it turns out, is a good way to catch the attention of infants whose tendency to attend has been affected by their hearing loss.

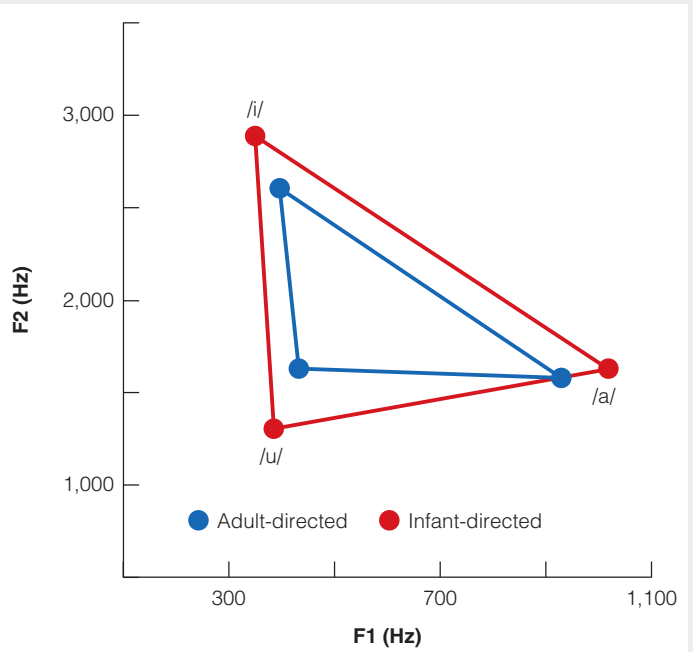

Figure 14.23 A "vowel triangle" in which the frequencies of the first formant (F1) and second formant (F2) are plotted for three vowel sounds, /i/, /a/, and /u/. The blue record is for adult-directed speech. The red record is for infant-directed speech. (From Golinkoff et al., 2015)

TEST YOURSELF 14.3

1. How did Davis use noise-vocoded speech to demonstrate how listeners can use information other than the acoustic signal to perceive speech?
2. Describe Robert Shannon's experiment on the temporal pattern of speech.
3. What did Broca and Wernicke discover about the physiology of speech perception?
4. Describe the "voice area" and "voice cells."
5. Describe the dual-stream model of speech perception.
6. Describe the Mesgarani electrode recording experiment. What did it demonstrate about neural responding to phonemes and to phonetic features?
7. Describe how cochlear implants work, and why the sounds they create are not the same as what normal-hearing people hear.
8. Why is it important to install CIs in deaf children at an early age?
9. What is infant-directed speech? How is it different from adult-directed speech?
10. Describe how the characteristics of infant-directed speech help infants to learn to perceive speech.

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THINK ABOUT IT

1. How well can computers recognize speech? You can research this question by talking to Siri, Alexa, or some other voice-recognition system, but instead of going out of your way to talk slowly and clearly, talk in a normal conversational voice or a little faster (but clearly enough that a human would still understand you), and see whether you can determine the limits of the computer's ability to understand speech. (p. 335)
2. How do you think your perception of speech would be affected if the phenomenon of categorical perception did not exist? (p. 340)

KEY TERMS

Acoustic signal (p. 336)
Acoustic stimulus (p. 336)
Adult-directed speech (p. 353)
Aphasia (p. 349)
Articulator (p. 336)
Audiovisual speech perception (p. 344)
Automatic speech recognition (ASR) (p. 335)
Broca's aphasia (p. 349)
Broca's area (p. 349)
Categorical perception (p. 340)
Coarticulation (p. 339)
Cochlear implant (p. 351)
Dual-stream model of speech perception (p. 350)
Formant (p. 336)
Formant transitions (p. 337)
Infant-directed speech (p. 353)
Manner of articulation (p. 337)
McGurk effect (p. 343)
Motor theory of speech perception (p. 340)
Multimodal (p. 343)
Noise-vocoded speech (p. 347)
Phoneme (p. 338)
Phonemic restoration effect (p. 344)
Phonetic boundary (p. 341)
Phonetic feature (p. 351)
Place of articulation (p. 337)
Sensorimotor hearing loss (p. 351)
Shadowing (p. 345)
Sound spectrogram (p. 336)
Speech segmentation (p. 345)
Speech spectrograph (p. 340)
Statistical learning (p. 346)
Transitional probabilities (p. 346)
Variability problem (p. 338)
Voice cells (p. 350)
Voice onset time (VOT) (p. 340)
Wernicke's aphasia (p. 349)
Wernicke's area (p. 349)
Word deafness (p. 350)

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This frog is stimulating receptors on the tip of the finger, which create perceptions of touch, pressure, and temperature. Different perceptions are created when the finger strokes the frog's skin. This chapter describes the perceptions associated with stimulation of the skin.

Tim Wright/Documentary Value/Corbis

Learning Objectives

After studying this chapter, you will be able to ...

- Describe the functions of the cutaneous senses.
- Describe the basic anatomy and functioning of the parts of the cutaneous system, ranging from skin to cortex.
- Describe the role of tactile exploration in perceiving details, vibrations, texture, and objects.
- Understand how receptors in the skin, brain connectivity and knowledge a person brings to a situation are involved in social touch.
- Describe the different kinds of pain and the gate-control theory of pain.
- Describe how top-down processes affect pain.
- Understand the connection between the brain and pain.
- Describe how pain can be affected by social touch and social situations.
- Understand the connection between pain and brain plasticity.

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CHAPTER 15

The Cutaneous Senses

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THINK ABOUT IT

Some Questions We Will Consider:

- Are there specialized receptors in the skin for sensing different tactile qualities? (p. 358)
- What is the most sensitive part of the body? (pp. 362, 364)
- Is it possible to reduce pain with your thoughts? (p. 375)
- What is the evidence that holding hands can reduce pain? (p. 379)

When asked which sense they would choose to lose, if they had to lose either vision, hearing, or touch, some people pick touch. This is understandable given the high value we place on seeing and hearing, but making a decision to lose the sense of touch would be a serious mistake. Although people who are blind or deaf can get along quite well, people with a rare condition that results in losing the ability to feel sensations though the skin often suffer constant bruises, burns, and broken bones in the absence of the warnings provided by touch and pain (Melzack & Wall, 1988; Rollman, 1991; Wall & Melzack, 1994).

But losing the sense of touch does more than increase the chance of injury. It also makes it difficult to interact with the environment because of the loss of feedback from the skin that accompanies many actions. As I type this, I hit my computer keys with just the right amount of force, because I can feel pressure when my fingers hit the keys. Without this feedback, typing and other actions that receive feedback from touch would become much more difficult. Experiments in which participants have had their hands temporarily anesthetized have shown that the resulting loss of feeling causes them to apply much more force than necessary when carrying

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out tasks with their fingers and hands (Avenanti et al., 2005; Monzée et al., 2003).

One of the most extreme examples of the effect of losing the ability to sense with the skin is the case of Ian Waterman, which we described in Chapter 7 (p. 162). As a result of an autoimmune reaction that destroyed most of the neurons that transmitted signals from his skin, joints, tendons, and muscles to his brain, he lost the ability to feel skin sensations so he couldn't feel his body when lying in bed, and he often used inappropriate force when grasping objects—sometimes gripping too tightly, and sometimes dropping objects because he hadn't gripped tightly enough.

To make things even worse, destruction of the nerves from his muscles, tendons, and joints eliminated Ian's ability to sense the position of his arms, legs, and body, so the only way he could carry out movements by visually monitoring the positions of his limbs and body.

Ian's problems were caused by a breakdown of his **somatosensory system**, which includes (1) the **cutaneous senses**, which are responsible for perceptions such as touch and pain that are usually caused by stimulation of the skin; (2) **proprioception**, the ability to sense the position of the body and limbs; and (3) **kinesthesis**, the ability to sense the movement of the body and limbs. In this chapter we will focus on the cutaneous senses, which are important not only for activities like grasping objects and protecting against damage to the skin, but also for motivating sexual activity (another reason picking touch as the sense to lose would be a mistake).

Not only are the perceptions we experience through our skin crucial for carrying out everyday activities and protecting ourselves from injury, but they can, under the right conditions, create good feelings! These good feelings come under the heading of *social touch*, which we will see can have beneficial effects beyond being pleasant. Considering all of the functions of the skin senses, we could make a good case for the idea that perceptions felt through the skin are as important both for day-to-day functioning and survival as are seeing and hearing.

Perception by the Skin and Hands

The cutaneous senses refer to everything we feel through the skin. Although touch and pain are the most obvious feelings involving the skin, there are many others, including pressure, vibration, tickle, temperature, and pleasure. We begin our discussion of the cutaneous senses by first describing the anatomy of the cutaneous system and then focusing on the sense of touch, which enables us to perceive properties of surfaces and objects such as details, vibrations, texture, and shape. In the second half of the chapter we will focus on the perception of pain.

15.1 Overview of the Cutaneous System

In this section we will describe some basic facts about the anatomy and functioning of the various parts of the cutaneous system.

The Skin

M. Comèl (1953) called the skin the "monumental facade of the human body" for good reason. It is the heaviest organ in the human body, and, if not the largest (the surface areas of the gastrointestinal tract and of the alveoli of the lungs exceed the surface area of the skin), it is certainly the most obvious, especially in humans, whose skin is not obscured by fur or large amounts of hair (Montagna & Parakkal, 1974).

In addition to its warning function, the skin also prevents body fluids from escaping and at the same time protects us by keeping bacteria, chemical agents, and dirt from penetrating our bodies. Skin maintains the integrity of what's inside and protects us from what's outside, but it also provides us with information about the various stimuli that contact it. The sun's rays heat our skin, and we feel warmth; a pinprick is painful; and when someone touches us, we experience pressure or other sensations.

On the surface of the skin is a layer of tough dead skin cells. (Try sticking a piece of cellophane tape onto your palm and pulling it off. The material that sticks to the tape is dead skin cells.) This layer of dead cells is part of the outer layer of skin, which is called the **epidermis**. Below the epidermis is another layer, called the **dermis** (**Figure 15.1**). Within the skin are **mechanoreceptors**, receptors that respond to mechanical stimulation such as pressure, stretching, and vibration.

Mechanoreceptors

Many of the tactile perceptions that we feel from stimulation of the skin can be traced to mechanoreceptors that are located in the epidermis and the dermis. Two mechanoreceptors, the **Merkel receptor** and the **Meissner corpuscle**, are located close to the surface of the skin, near the epidermis. Because they are located close to the surface, these receptors have small receptive fields. (Just as a visual receptive field is the area of *retina* which, when stimulated, causes firing of a neuron (p. 55), a **cutaneous receptive field** is the area of *skin* which, when stimulated, influences the firing of the neuron.)

Figure 15.1 shows the structure and firing of the Merkel and Meissner receptors in response to a pressure stimulus that is presented and then removed (blue line). Because the nerve fiber associated with the slowly adapting Merkel receptor fires continuously, as long as the stimulus is on, it is called a **slowly adapting (SA1) fiber**. Because the nerve fiber associated with the rapidly adapting Meissner corpuscle fires only when the stimulus is first applied and when it is removed, it is called a

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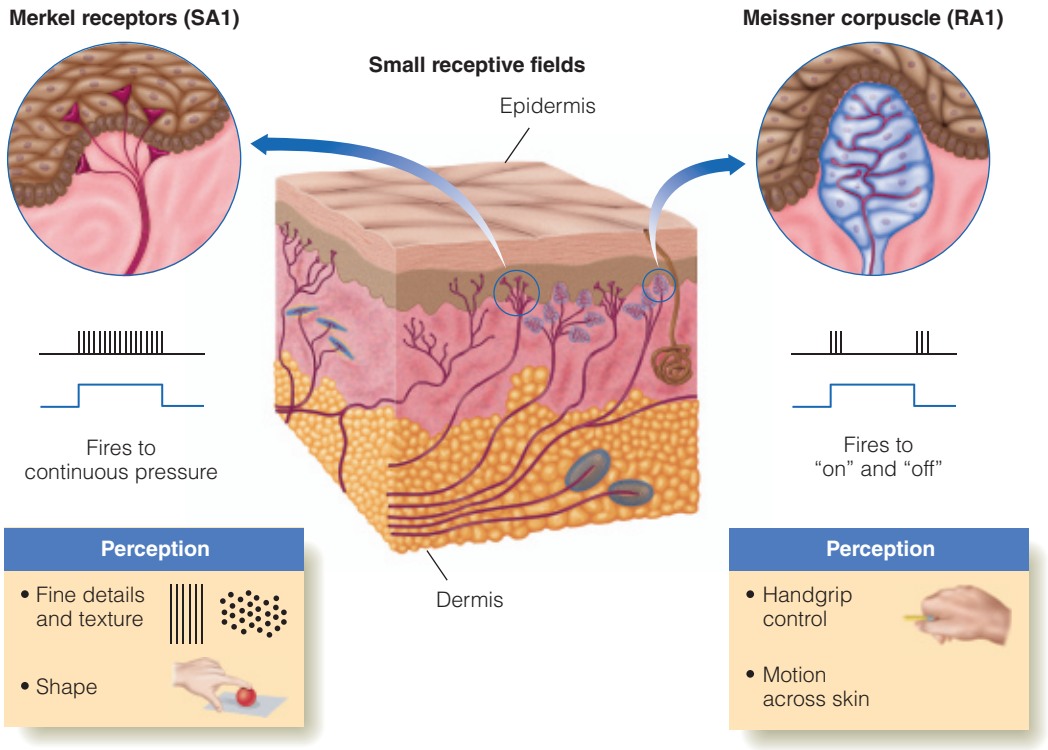

Figure 15.1 A cross section of glabrous (without hairs or projections) skin, showing the layers of the skin and the structure, firing properties, and perceptions associated with the Merkel receptor (SA1) and Meissner corpuscle (RA1)—two mechanoreceptors near the surface of the skin.

rapidly adapting (RA1) fiber. The types of perception associated with the Merkel receptor/SA1 fiber are details, shape, and texture, and with the Meissner corpuscle/RA1 fiber, controlling handgrip and perceiving motion across the skin.

Like the Merkel receptors, the Ruffini cylinder is a slowly adapting (SA2) fiber, which responds continuously to stimulation. Like the Meissner corpuscle, the Pacinian corpuscle is a rapidly adapting fiber (RA2 or PC) which responds when the stimulus is applied or removed. Both the Ruffini cylinder and Pacinian corpuscle are located deep in the skin (**Figure 15.2**), so they have larger receptive fields. The Ruffini cylinder is associated with perceiving stretching of the skin, the Pacinian corpuscle with sensing rapid vibrations and fine texture.[1]

Our description has associated each receptor/fiber type with specific types of stimulation. However, when we consider how neurons fire when fingers move across natural textures, we will see that the perception of texture often involves the coordinated activity of different types of neurons working together.

Pathways From Skin to Cortex and Within the Cortex

The receptors for the other senses are localized in one area—the eye (vision), the ear (hearing), the nose (olfaction), and the mouth (taste)—but cutaneous receptors in the skin are distributed over the whole body. This wide distribution, plus the fact that signals must reach the brain before stimulation of the skin can be perceived, creates a travel situation we might call "journey of the long-distance nerve impulses," especially for signals that must travel from the fingertips or toes to the brain.

Signals from all over the body are conducted from the skin to the spinal cord, which consists of 31 segments, each of which receives signals through a bundle of fibers called the *dorsal root* (**Figure 15.3**). After the signals enter the spinal cord, nerve fibers transmit them to the brain along two major pathways: the medial lemniscal pathway and the spinothalamic pathway. The lemniscal pathway has large fibers that carry signals related to sensing the positions of the limbs (proprioception) and perceiving touch. These large fibers transmit signals at high speed, which is important for and reacting to touch. The spinothalamic pathway consists of smaller fibers that transmit signals related to temperature and pain. The case of Ian Waterman illustrates this separation in function, because although he lost the ability to feel touch and to sense the positions of his limbs (lemniscal pathway), he was still able to sense pain and temperature (spinothalamic pathway).

Fibers from both pathways cross over to the other side of the body during their upward journey and synapse in the thalamus. (Remember that fibers from the retina and the cochlea also synapse in the thalamus, in the *lateral geniculate nucleus* for vision and the *medial geniculate nucleus* for hearing. Most of the fibers in the cutaneous system synapse

[1]Although Michael Paré and coworkers (2002) have reported that there are no Ruffini receptors in the finger pads of monkeys, Ruffini cylinders are still included in most lists of glabrous (nonhairy) skin receptors, so they are included here.

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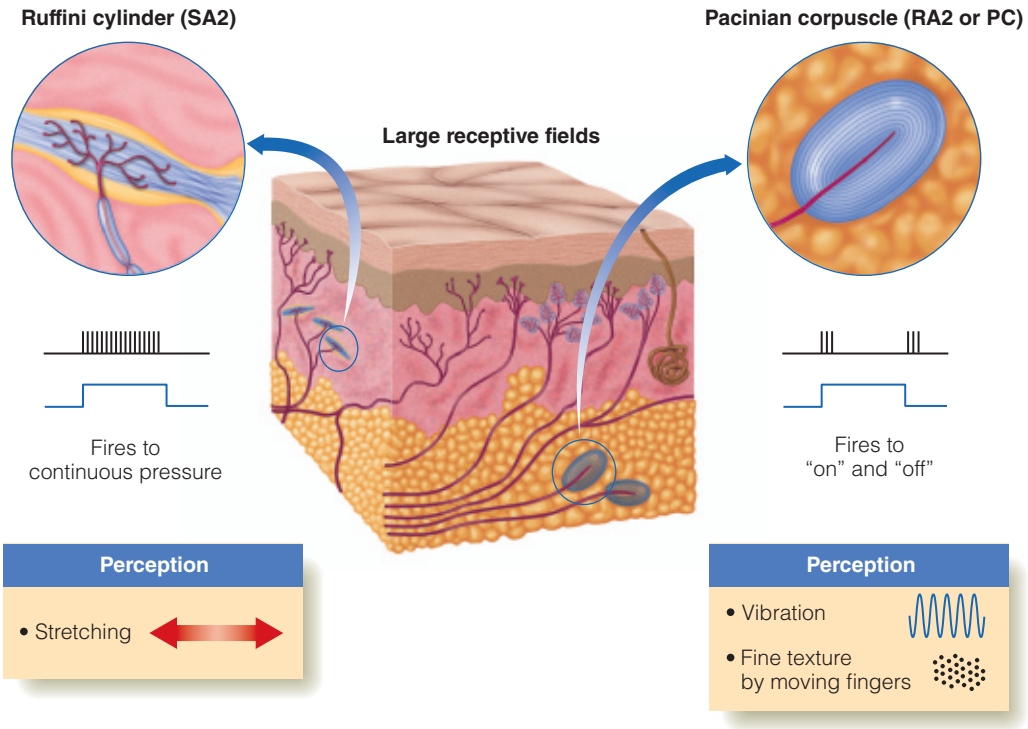

Figure 15.2 A cross section of glabrous skin, showing the structure, firing properties, and perceptions associated with the Ruffini cylinder (SA2) and the Pacinian corpuscle (RA2 or PC)—two mechanoreceptors that are deeper in the skin.

in the ventrolateral nucleus of the thalamus.) Because the signals in the spinal cord have crossed over to the opposite side of the body, signals originating from the left side of the body reach the thalamus in the right hemisphere of the brain, and signals from the right side of the body reach the left hemisphere.

The idea of two pathways conducting cutaneous signals to the thalamus and then to the somatosensory cortex supports the idea that different pathways serve different sensations. But it is important to realize that the cutaneous pathways and structures within the brain that are far more complex than the picture in Figure 15.3. This complexity is illustrated in

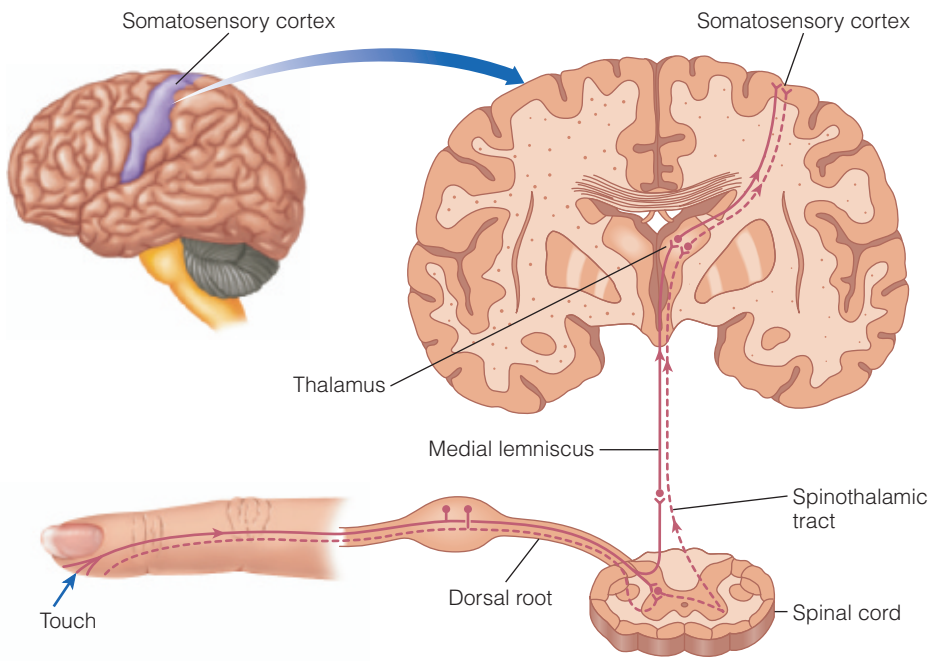

Figure 15.3 The pathway from receptors in the skin to the somatosensory receiving area of the cortex. The fiber carrying signals from a receptor in the finger enters the spinal cord through the dorsal root. The signals then travel up the spinal cord along two pathways: the medial lemniscus and the spinothalamic tract. These pathways synapse in the thalamus and then send signals to the somatosensory cortex in the parietal lobe.

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Figure 15.4, which shows multiple brain areas that are associated with cutaneous functions (Bushnell et al., 2013).

Somatosensory Areas in the Cortex

Two of the areas that receive signals from the thalamus are the **primary somatosensory cortex (S1)** in the parietal lobe and the **secondary somatosensory cortex (S2)** (Rowe et al., 1996; Turman et al., 1998). Signals also travel between S1 and S2 and to a network of other areas in the brain in additional pathways that are not shown here (Avanzini et al., 2016; Rullman et al., 2019). Two of the structures in Figure 15.4, in addition to S1 and S2, that we will be encountering later in the chapter are the *insula*, which is important for sensing light touch, and the *anterior cingulate cortex (ACC)*, which is involved in pain.

An important characteristic of the somatosensory cortex is that it is organized into maps that correspond to locations on the body. The story behind the discovery of these maps is an interesting one that begins in the 1860s, when British neurologist Hughlings Jackson observed that in some cases of epilepsy, his patients' seizures progressed over the body in an orderly way, with a seizure in one body part being followed by a seizure in a neighboring body part, and so on (Jackson, 1870). This sequence, which came to be known as "the Jacksonian march,"

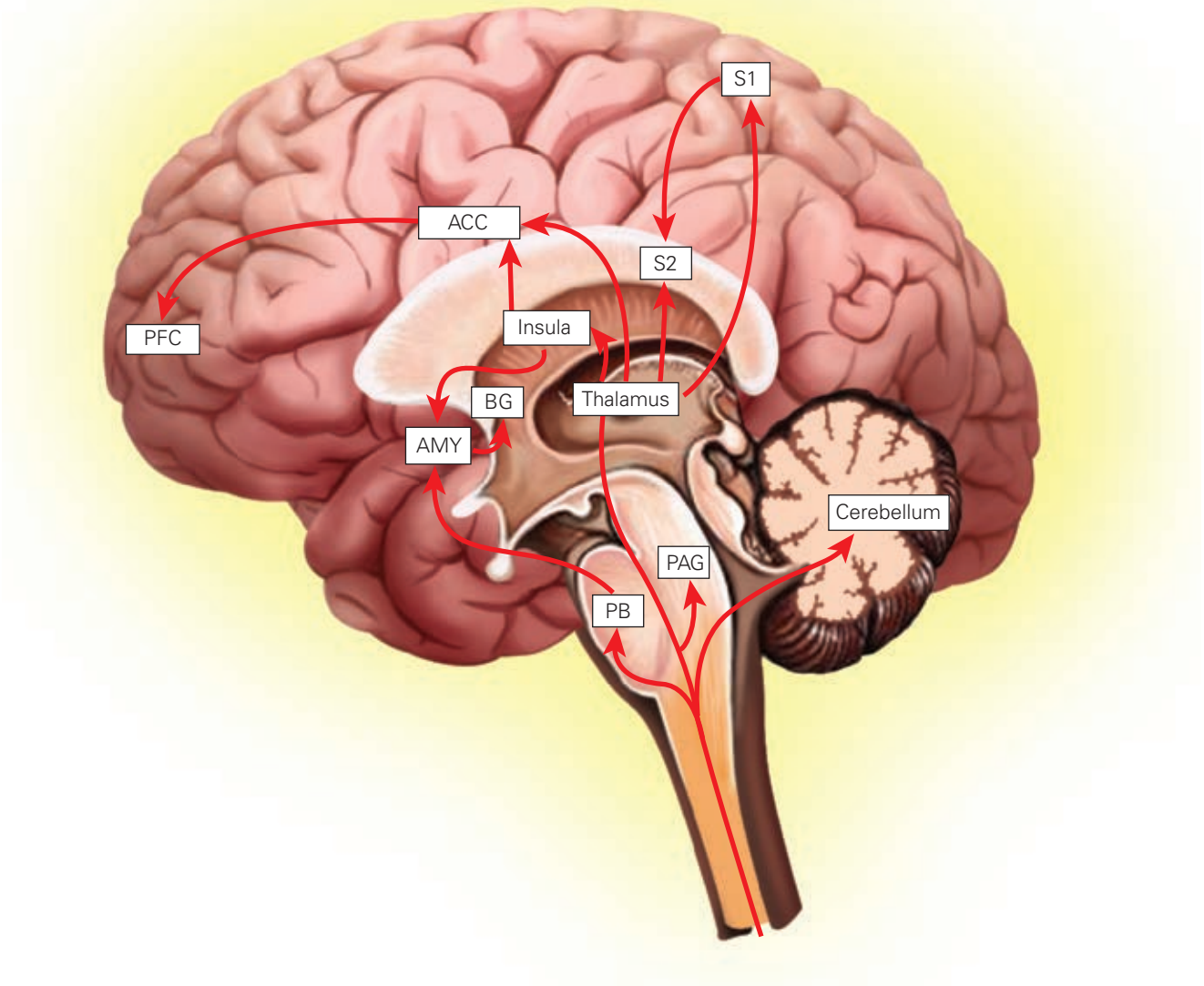

Figure 15.4 Some of the brain structures associated with the cutaneous system. We will be considering the structures that are labeled: primary somatosensory cortex (S1), secondary somatosensory cortex (S2), anterior cingulate cortex (ACC), and the insula. (Bushnell et al., 2013)

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suggested that the seizures reflected the spread of neural activity across maps in the motor area of the brain (Berkowitz, 2018; Harding-Forrester & Feldman, 2018). Sixty-seven years later, Wilder Penfield and Edwin Boldrey (1937) measured the map of the somatosensory cortex by stimulating points on the brain of awake patients who were having brain surgery to relieve symptoms of epilepsy (Penfield & Rasmussen, 1950). Note that there are no pain receptors in the brain, so the patients cannot feel the surgery.

When Penfield stimulated points on the primary somatosensory cortex (S1) and asked patients to report what they perceived, they reported sensations such as tingling and touch on various parts of their body. Penfield found that stimulating the ventral part of S1 (lower on the parietal lobe) caused sensations on the lips and face, stimulating higher on S1 caused sensations in the hands and fingers, and stimulating the dorsal S1 caused sensations in the legs and feet.

The resulting body map, shown in **Figure 15.5**, is called the homunculus, Latin for "little man." The homunculus shows that adjacent areas of the skin project to adjacent areas in the brain, and that some areas on the skin are represented by a disproportionately large area of the brain. The area devoted to the thumb, for example, is as large as the area devoted to the entire forearm. This result is analogous to the cortical magnification factor in vision (see page 75), in which receptors in the fovea, which are responsible for perceiving visual details, are allotted a disproportionate area on the visual cortex. Similarly, parts of the body such as the fingers, which are used to detect details through the sense of touch, are allotted a disproportionate area on the somatosensory cortex (Duncan & Boynton, 2007). A similar body map also occurs in the secondary somatosensory cortex (S2).

This description in terms of S1 and S2 and the homunculus is accurate but simplified. Recent research has shown that S1 is divided into four interconnected areas, each with its own body map and its own functions (Keysers et al., 2010). For example, the area in S1 involved in perceiving touch is connected to another area that is involved in *haptics* (exploring objects with the hand). Finally, there are other areas that we will discuss when we consider pain later in the chapter. The fact that the cutaneous system involves numerous areas of the brain which communicate with each other over many pathways isn't surprising when we consider the many different qualities that are sensed by the skin.

Now that we've described the cutaneous receptors and some of the brain areas that are activated by signals arriving from the receptors, we will consider how we perceive qualities such as details, vibration, and texture.

15.2 Perceiving Details

One of the most impressive examples of perceiving details with the skin is provided by Braille, the system of raised dots that enables blind people to read with their fingertips. A Braille character consists of a cell made up of one to six dots. Different arrangements of dots and blank spaces represent letters of the alphabet, as shown in **Figure 15.6**; additional characters

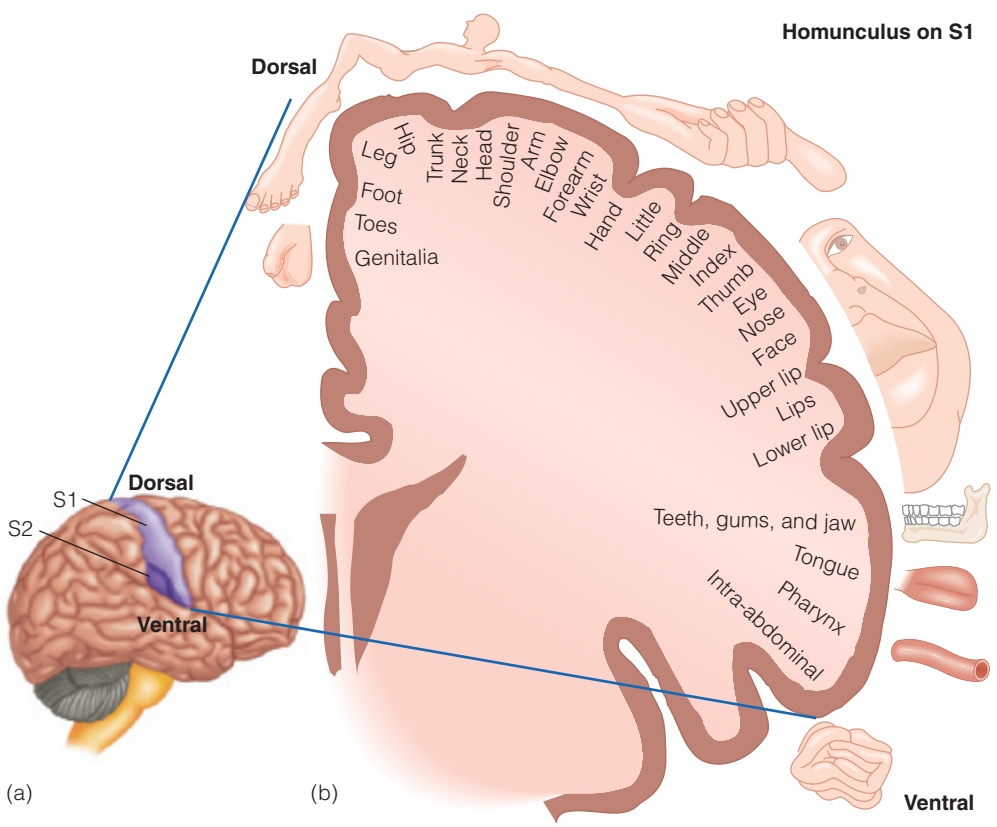

Figure 15.5 (a) The somatosensory cortex in the parietal lobe. The primary somatosensory area, S1 (light purple), receives inputs from the ventrolateral nucleus of the thalamus. The secondary somatosensory area, S2 (dark purple), is partially hidden behind the temporal lobe. (b) The sensory homunculus on the somatosensory cortex. Parts of the body with the highest tactile acuity are represented by larger areas on the cortex. (Adapted from Penfield & Rasmussen, 1950)

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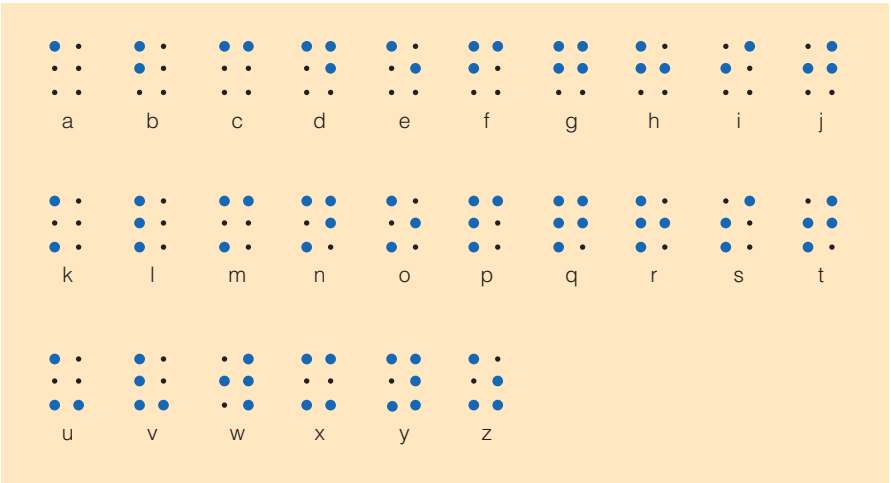

Figure 15.6 The Braille alphabet consists of raised dots in a 2 × 3 matrix. The large blue dots indicate the location of the raised dot for each letter. Blind people read these dots by scanning them with their fingertips.

represent numbers, punctuation marks, and common speech sounds and words.

Experienced Braille readers can read at a rate of about 100 words per minute, slower than the rate for visual reading, which averages about 250 to 300 words per minute, but impressive nonetheless when we consider that a Braille reader transforms an array of raised dots into information that goes far beyond simply feeling sensations on the skin.

The ability of Braille readers to identify patterns of small raised dots based on the sense of touch depends on tactile detail perception. The first step in describing research on tactile detail perception is to consider how researchers have measured **tactile acuity**—the capacity to detect details of stimuli presented to the skin.

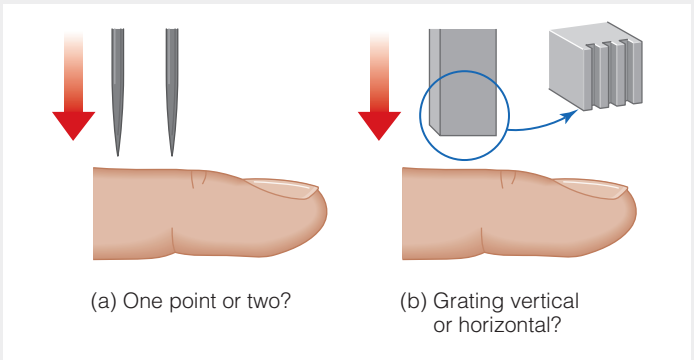

Figure 15.7 Methods for determining tactile acuity: (a) two-point threshold; (b) grating acuity.

METHOD | Measuring Tactile Acuity

Just as there are a number of different kinds of eye charts for determining a person's visual acuity, there are a number of ways to measure a person's tactile acuity. The classic method of measuring tactile acuity is the two-point threshold, the minimum separation between two points on the skin that when stimulated is perceived as two points (**Figure 15.7a**). The two-point threshold is measured by gently touching the skin with two points, such as the points of a drawing compass, and having the person indicate whether he or she feels one point or two.

The two-point threshold was the main measure of acuity in most of the early research on touch. Recently, however, other methods have been introduced. Grating acuity is measured by pressing a grooved stimulus like the one in **Figure 15.7b** onto the skin and asking the person to indicate the orientation of the grating. Acuity is measured by determining the narrowest spacing for which orientation can be accurately judged. Finally, acuity can also be measured by pushing raised patterns such as letters onto the skin and determining the smallest sized pattern or letter that can be identified (Cholewaik & Collins, 2003; Craig & Lyle, 2001, 2002).

As we consider the role of both receptor mechanisms and cortical mechanisms in determining tactile acuity, we will see that there are a number of parallels between the cutaneous system and the visual system.

Receptor Mechanisms for Tactile Acuity

The properties of the receptors are one of the things that determine what we experience when the skin is stimulated. We will illustrate this by first focusing on the connection between the Merkel receptor and associated fibers and tactile acuity. **Figure 15.8a** shows how the fiber associated with a Merkel receptor fires in response to a grooved stimulus pushed into the skin. Notice that the firing of the fiber reflects the pattern of the grooved stimuli. This indicates that the firing of the Merkel receptor's fiber signals details (Johnson, 2002; Phillips & Johnson, 1981). For comparison, **Figure 15.8b** shows the firing of the fiber associated with the Pacinian corpuscle. The lack of match between the grooved pattern and the firing indicates that this receptor is not sensitive to the details of patterns that are pushed onto the skin.

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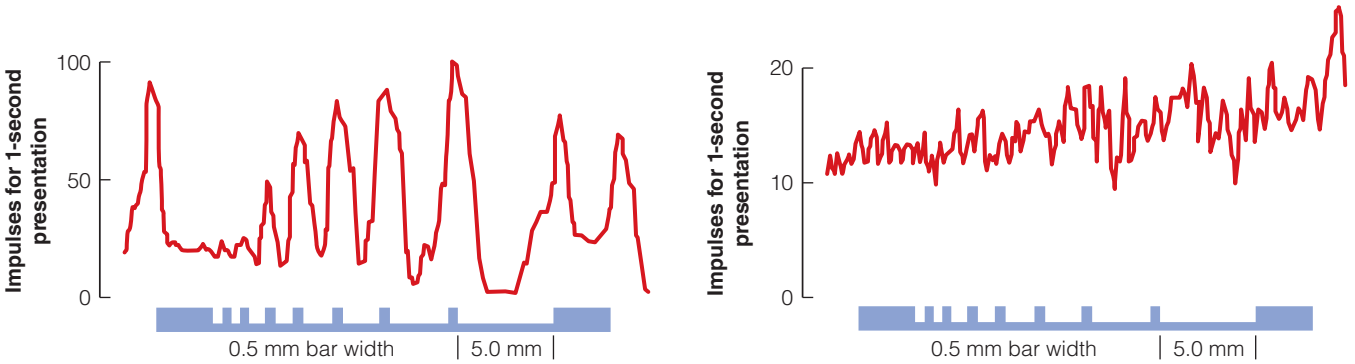

Figure 15.8 Firing to the grooved stimulus pattern of (a) the fiber associated with a Merkel receptor and (b) the fiber associated with a Pacinian corpuscle receptor. The response to each groove width was recorded during a 1-second indentation for each bar width, so these graphs represent the results for a number of presentations. (Adapted from Phillips & Johnson, 1981)

It is not surprising that there is a high density of Merkel receptors in the fingertips, because the fingertips are the parts of the body that are most sensitive to details (Vallbo & Johansson, 1978). The relationship between locations on the body and sensitivity to detail has been studied psychophysically by measuring the two-point threshold on different parts of the body. Try this yourself by doing the following demonstration.

DEMONSTRATION | Comparing Two-Point Thresholds

To measure two-point thresholds on different parts of the body, hold two pencils side by side (or better yet, use a drawing compass) so that their points are about 12 mm (0.5 in.) apart; then touch both points simultaneously to the tip of your thumb and determine whether you feel two points. If you feel only one, increase the distance between the pencil points until you feel two; then note the distance between the points. Now move the pencil points to the underside of your forearm. With the points about 12 mm apart (or at the smallest separation you felt as two points on your thumb), touch them to your forearm and note whether you feel one point or two. If you feel only one, how much must you increase the separation before you feel two?

A comparison of grating acuity on different parts of the hand shows that better acuity is associated with less spacing between Merkel receptors (**Figure 15.9**). But receptor spacing isn't the whole story, because the cortex also plays a role in determining tactile acuity (Duncan & Boynton, 2007).

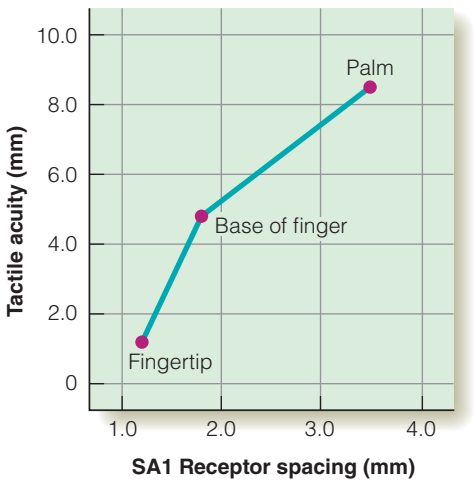

Figure 15.9 Correlation between density of Merkel receptors and tactile acuity. (From Craig & Lyle, 2002)

Cortical Mechanisms for Tactile Acuity

Just as there is a parallel between tactile acuity and receptor density, there is also a parallel between tactile acuity and the representation of the body in the brain. **Table 15.1** indicates the two-point threshold measured on different parts of the male body. By comparing these two-point thresholds to how different parts of the body are represented in the brain (Figure 15.5a), we can see that regions of high acuity, like the fingers and lips, are represented by larger areas on the cortex. As we mentioned earlier, when we described the homunculus, "magnification" of the representation on the brain of parts of the body such as the fingertips parallels the magnification

Table 15.1 Two-Point Thresholds on Different Parts of the Male Body

PART OF BODY	THRESHOLD (MM)
Fingers	4
Upper lip	8
Big toe	9
Upper arm	46
Back	42
Thigh	44

Data from Weinstein, 1968.

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factor in vision (p. 75). The map of the body on the brain is enlarged to provide the extra neural processing that enables us to accurately sense fine details with our fingers and other parts of the body.

Another way to demonstrate the connection between cortical mechanisms and acuity is to determine the receptive fields of neurons in different parts of the cortical homunculus. **Figure 15.10**, which shows the sizes of receptive fields from cortical neurons that receive signals from a monkey's fingers (**Figure 15.10a**), hand (**Figure 15.10b**), and arm (**Figure 15.10c**), indicates that cortical neurons representing parts of the body with better acuity, such as the fingers, have smaller receptive fields. This means that two points that are close together on the fingers might fall on receptive fields that don't overlap (as indicated by the two arrows in Figure 15.10a) and so would cause neurons that are separated in the cortex to fire (**Figure 15.10d**). However, two points with the same separation when applied to the arm are likely to fall on receptive fields that overlap (see arrows in Figure 15.10c) and so could cause neurons that are not separated in the cortex to fire (Figure 15.10d). Thus, the small receptive fields of neurons receiving signals from the fingers translates into more separation on the cortex, which enhances the ability to feel two close-together points on the skin as two separate points.

15.3 Perceiving Vibration and Texture

The skin is capable of detecting not only spatial details of objects, but other qualities as well. When you place your hands on mechanical devices that produce vibration, such as a car, a lawnmower, or an electric toothbrush, you can sense these vibrations with your fingers and hands.

Vibration of the Skin

The mechanoreceptor that is primarily responsible for sensing vibration is the Pacinian corpuscle. One piece of evidence linking the Pacinian corpuscle to vibration is that recording from fibers associated with the corpuscle shows that these fibers respond poorly to slow or constant pushing but respond well to high rates of vibration.

Why do the Pacinian corpuscle fibers respond well to rapid vibration? The answer to this question is that the presence of the corpuscle surrounding the nerve fiber determines which pressure stimuli actually reach the fiber. The corpuscle, which consists of a series of layers, like an onion, with fluid between each layer, transmits rapidly repeated pressure, like vibration, to the nerve fiber, as shown in **Figure 15.11a**, but does not transmit continuous pressure, as shown in **Figure 15.11b**. Thus, the corpuscle causes the fiber to receive rapid changes in pressure, but not to receive continuous pressure.

Because the Pacinian corpuscle does not transmit continuous pressure to the fiber, presenting continuous pressure to the corpuscle should cause no response in the fiber. This is exactly what Werner Lowenstein (1960) observed in a classic experiment, in which he showed that when pressure was applied to the corpuscle (at A in **Figure 15.11c**), the fiber responded when the pressure was first applied and when it was removed, but it did not respond to continuous pressure. But when Lowenstein dissected away the corpuscle and applied pressure directly to the fiber (at B in Figure 15.11c), the fiber fired to the continuous pressure. Lowenstein concluded from this result that properties of the corpuscle cause the fiber to respond poorly to continuous stimulation, such as sustained pressure, but to respond well to changes in stimulation that occur at the beginning and end of a pressure stimulus or when stimulation is changing rapidly, as occurs in vibration. As we now consider the perception of surface texture, we will see that vibration plays a role in perceiving fine textures.

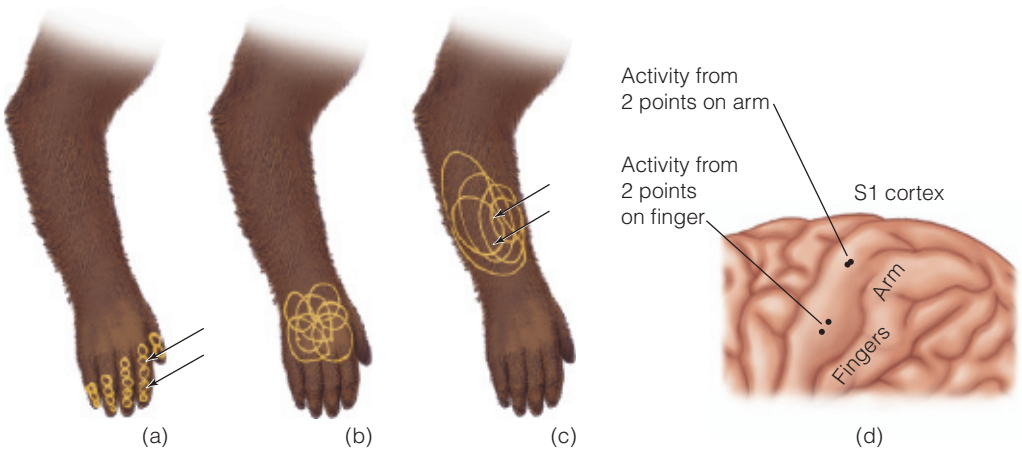

Figure 15.10 Receptive fields of monkey cortical neurons that fire (a) when the fingers are stimulated, (b) when the hand is stimulated, and (c) when the arm is stimulated. (d) Stimulation of two nearby points on the finger causes separated activation on the finger area of the cortex, but stimulation of two nearby points on the arm causes overlapping activation in the arm area of the cortex. (From Kandel & Jessell, 1991)

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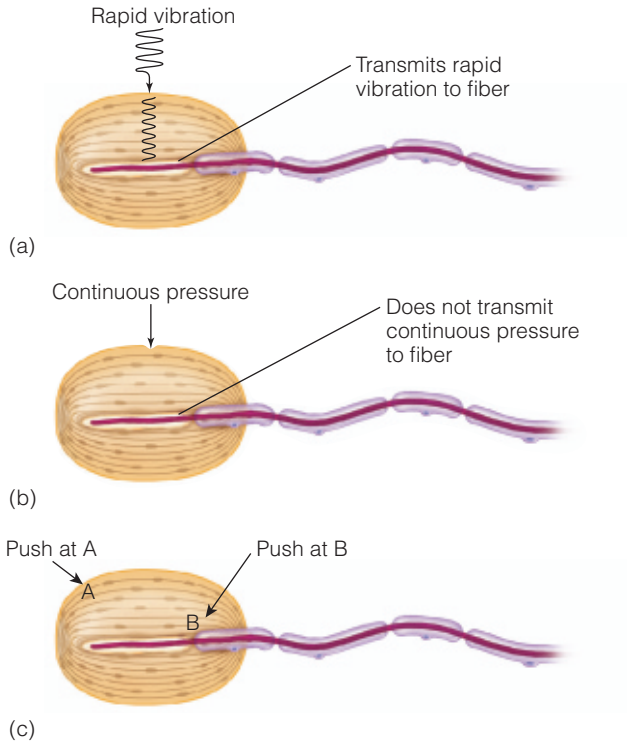

Figure 15.11 (a) When a vibrating pressure stimulus is applied to the Pacinian corpuscle, it transmits these pressure vibrations to the nerve fiber. (b) When a continuous pressure stimulus is applied to the Pacinian corpuscle, it does not transmit the continuous pressure to the fiber. (c) Lowenstein determined how the fiber fired to stimulation of the corpuscle (at A) and to direct stimulation of the fiber (at B). (Adapted from Lowenstein, 1960)

Surface Texture

Surface texture is the physical texture of a surface created by peaks and valleys. As can be seen in **Figure 15.12**, visual inspection can be a poor way of determining surface texture because seeing texture depends on the light–dark pattern determined by the angle of illumination. Thus, although the visually perceived texture of the two sides of the post in Figure 15.12 looks very different, moving the fingers across the two surfaces reveals that their texture is the same.

Research on texture perception tells an interesting story, extending from 1925 to the present, that illustrates how psychophysics can be used to understand perceptual mechanisms. In 1925, David Katz proposed what is now called the **duplex theory of texture perception**, which states that our perception of texture depends on both spatial cues and temporal cues (Hollins & Risner, 2000; Katz, 1925/1989).

Spatial cues are provided by relatively large surface elements, such as bumps and grooves, that can be felt both when the skin moves across the surface elements and when it is pressed onto the elements. These cues result in feeling different shapes, sizes, and distributions of these surface elements. An example of spatial cues is perceiving a coarse texture such as Braille dots or the texture you feel when you touch the teeth of a comb.

Temporal cues occur when the skin moves across a textured surface like fine sandpaper. This type of cue provides information in the form of vibrations that occur as a result of the movement over the surface. Temporal cues are responsible for our perception of fine texture that cannot be detected unless the fingers are moving across the surface.

Although Katz proposed that texture perception is determined by both spatial and temporal cues, research on texture perception has, until recently, focused on spatial cues. However, Mark Hollins and Ryan Risner (2000) presented evidence for the role of temporal cues by showing that when participants touched surfaces without moving their fingers and judge "roughness" using the procedure of magnitude estimation (see Chapter 1, page 16; Appendix B, page 418), they sensed little difference between two fine textures (particle sizes of 10 μm and 100 μm). However, when participants were allowed to move their fingers across the surface, they could detect the difference between the fine textures. Thus, movement, which generates vibration as the skin scans a surface, makes it possible to sense the roughness of fine surfaces.

These results and the results of other behavioral experiments (Hollins et al., 2002) support the duplex theory of

Figure 15.12 The post in (a) is illuminated from the left. The close-up in (b) shows how the visual perception of texture is influenced by illumination. Although the surface on the right side of the pole appears rougher than on the left, the surface textures of the two sides are identical.

Courtesy of Bruce Goldstein

(a)

Courtesy of Bruce Goldstein

(b)

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perception—that the perception of coarse textures is determined by spatial cues and of fine textures by temporal (vibration) cues (also see Weber et al., 2013).

Additional evidence for the role of temporal cues in perceiving texture has been provided by research that shows that vibrations are important for perceiving textures not only when people explore a surface directly with their fingers, but also when they make contact with a surface indirectly, through the use of tools. You can experience this yourself by doing the following demonstration.

DEMONSTRATION | Perceiving Texture With a Pen

Turn your pen over (or cap it) so you can use it as a "probe" (without writing on things). Hold the pen at one end and move the other end over something smooth, such as your desk or a piece of paper. As you do this, notice that you can sense the smoothness of the page, even though you are not directly touching it. Then, try the same thing on a rougher surface, such as a rug, fabric, or concrete.

Your ability to detect differences in texture by running a pen (or some other "tool," such as a stick) over a surface is determined by vibrations transmitted through the tool to your skin (Klatzky et al., 2003). The most remarkable thing about perceiving texture with a tool is that what you perceive is not the vibrations but the texture of the surface, even though you are feeling the surface remotely, with the tip of the tool (Carello & Turvey, 2004).

Cortical Responses to Surface Texture Justin Lieber and Sliman Bensmaia (2019) studied how textures are represented in the brain by training monkeys to place their fingers on a rotating drum like the one in **Figure 15.13a**. Textures ranged from very fine (micorsuede) to coarse (dots spaced 5 mm apart. **Figure 15.13b** shows a monkey having a texture scanned across its fingertip. **Figure 15.13c** shows the responses of five neurons in the somatosensory cortex to six different textures. These patterns show that (1) different textures caused different firing patterns in an individual neuron (compare records from left to right, across textures, for a particular neuron), and (2) different neurons responded differently to the same texture (compare records from top to bottom for a specific texture).

These results showed that texture is represented in the cortex by the pattern of firing of many neurons. In addition, Lieber and Bensmaia found that cortical neurons that fired best to coarse textures received input from SA1 neurons in the skin (Merkel receptors) and neurons that fired best to fine textures received input from PC receptors (Pacinian corpuscles).

Figure 15.13 (a) Experimental apparatus used by Lieber and Bensmaia (2019), which, when rotated, scanned different textures across fingertips. (b) A monkey having its finger scanned. (c) Firing patterns of five different neurons (numbers on the left) to six textures.

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TEST YOURSELF 15.1

1. Describe the four types of mechanoreceptors in the skin, indicating (a) their appearance, (b) where they are located, (c) how they respond to pressure, (d) the sizes of their receptive fields, (e) the type of perception associated with each receptor, and (f) the type of fiber associated with each receptor.
2. Where is the cortical receiving area for touch, and what does the map of the body on the cortical receiving area look like? How can this map be changed by experience?
3. How is tactile acuity measured, and what are the receptor and cortical mechanisms that serve tactile acuity?
4. Which receptor is primarily responsible for the perception of vibration? Describe the experiment that showed that the presence of the receptor structure determines how the fiber fires.
5. What is the duplex theory of texture perception? Describe the series of behavioral experiments that led to the conclusion that vibration is responsible for perceiving fine textures and observations that have been made about the experience of exploring an object with a probe.
6. Describe the experiment which showed how monkey cortical neurons respond to texture. What do the results indicate about how texture is represented in the cortex?

15.4 Perceiving Objects

Imagine that you and a friend are at the seashore. Your friend knows something about shells from the small collection he has accumulated over the years, so as an experiment you decide to determine how well he can identify different types of shells by using his sense of touch alone. When you blindfold your friend and hand him a snail shell and a crab shell, he has no trouble identifying the shells as a snail and a crab. But when you hand him shells of different types of snails that are very similar, he finds that identifying the different types of snails is much more difficult.

Geerat Vermeij, blind at the age of 4 from a childhood eye disease and currently Distinguished Professor of Marine Ecology and Paleoecology at the University of California at Davis, describes his experience when confronted with a similar task. This experience occurred when he was being interviewed by Edgar Boell, who was considering Vermeij's application for graduate study in the biology department at Yale. Wondering whether Geerat's blindness would disqualify him from graduate study, Boell took Vermeij to the museum, introduced him to the curator, and handed him a shell. Here is what happened next, as told by Vermeij (1997):

> "Here's something. Do you know what it is?" Boell asked as he handed me a specimen.
>
> My fingers and mind raced. Widely separated ribs parallel to outer lip; large aperture; low spire; glossy; ribs reflected backward. "It's a Harpa," I replied tentatively. "It must be Harpa major." Right so far.
>
> "How about this one?" inquired Boell, as another fine shell changed hands. Smooth, sleek, channeled suture, narrow opening; could be any olive. "It's an olive. I'm pretty sure it's Oliva sayana, the common one from Florida, but they all look alike."
>
> Both men were momentarily speechless. They had planned this little exercise all along to call my bluff. Now that I had passed, Boell had undergone an instant metamorphosis. Beaming with enthusiasm and warmth, he promised me his full support. (pp. 79–80)

Vermeij received his PhD from Yale and is now a world-renowned expert on marine mollusks. His ability to identify objects and their features by touch is an example of **active touch**—touch in which a person actively explores an object, usually with fingers and hands. In contrast, **passive touch** occurs when touch stimuli are applied to the skin, as when two points are pushed onto the skin to determine the two-point threshold. The following demonstration compares the ability to identify objects using active touch and passive touch.

DEMONSTRATION | Identifying Objects

Ask another person to select five or six small objects for you to identify. Close your eyes and have the person place an object in your hand. In the active condition your job is to identify the object by touch alone, by moving your fingers and hand over the object. As you do this, be aware of what you are experiencing: your finger and hand movements, the sensations you are feeling, and what you are thinking. Do this for three objects. Then, in the passive condition, hold out your hand, keeping it still, with fingers outstretched, and let the person move each of the remaining objects around on your hand, moving their surfaces and contours across your skin. Your task is the same as before: to identify the object and to pay attention to what you are experiencing as the object is moved across your hand.

You may have noticed that in the active condition, in which you moved your fingers across the object, you were much more involved in the process than in the passive condition, and you had more control over what parts of the objects to which you were exposed. The active part of the demonstration involved **haptic perception**—perception in which three-dimensional objects are explored with the fingers and hand.

Identifying Objects by Haptic Exploration

Haptic perception is an example of a situation in which a number of different systems are interacting with each other. As you manipulated the objects in the first part of the demonstration above, you were using three distinct systems to arrive at your goal of identifying the objects: (1) the *sensory system*, which was involved in detecting cutaneous sensations such as touch,

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temperature, and texture and the movements and positions of your fingers and hands; (2) the *motor system*, which was involved in moving your fingers and hands; and (3) the *cognitive system*, which was involved in thinking about the information provided by the sensory and motor systems.

Haptic perception is an extremely complex process because the sensory, motor, and cognitive systems must all work together. For example, the motor system's control of finger and hand movements is guided by cutaneous feelings in the fingers and the hands, by your sense of the positions of the fingers and hands, and by thought processes that determine what information is needed about the object in order to identify it.

These processes working together create an experience of active touch that is quite different from the experience of passive touch. J. J. Gibson (1962), who championed the importance of movement in perception (see Chapter 7, page 150, and Chapter 8, page 181), compared the experience of active and passive touch by noting that we tend to relate passive touch to the sensation experienced in the skin, whereas we relate active touch to the object being touched. For example, if someone pushes a pointed object into your skin, you might say, "I feel a pricking sensation on my skin"; if, however, you push on the tip of the pointed object yourself, you might say, "I feel a pointed object" (Kruger, 1970). Thus, for passive touch you experience stimulation of the skin, and for active touch you experience the objects you are touching.

Psychophysical research has shown that people can accurately identify most common objects within 1 or 2 seconds using active touch (Klatzky et al., 1985). When Susan Lederman and Roberta Klatzky (1987, 1990) observed participants' hand movements as they made these identifications, they found that people use a number of distinctive movements, which they called exploratory procedures (EPs), and that the types of EPs used depend on the object qualities the participants are asked to judge.

Figure 15.14 shows four of the EPs observed by Lederman and Klatzky. People tend to use just one or two EPs to determine a particular quality. For example, people use mainly lateral motion and contour following to judge texture, and they use enclosure and contour following to judge exact shape.

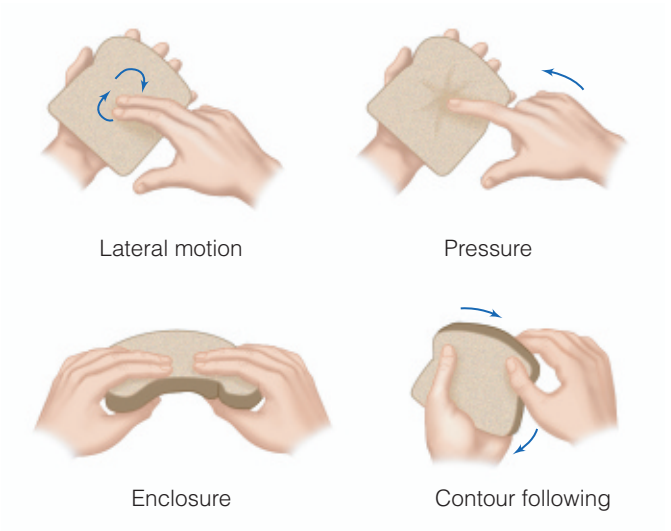

Figure 15.14 Some of the exploratory procedures (EPs) observed by Lederman and Klatzky as participants identified objects. (From Lederman & Klatzky, 1987)

The Cortical Physiology of Tactile Object Perception

Exploring objects with our fingers and hands activates mechanoreceptors that send signals toward the cortex. When these signals reach the cortex, they eventually activate specialized neurons.

Cortical Neurons Are Specialized Moving from mechanoreceptor fibers in the fingers toward the brain, neurons become more specialized. This is similar to what occurs in the visual system. Neurons in the ventral posterior nucleus, which is the tactile area of the thalamus, have center-surround receptive fields that are similar to the center-surround receptive fields in the lateral geniculate nucleus, which is the visual area of the thalamus (Mountcastle & Powell, 1959; **Figure 15.15**).

In the cortex, we find some neurons with center-surround receptive fields and others that respond to more specialized stimulation of the skin. **Figure 15.16** shows stimuli that cause neurons in the monkey's somatosensory cortex to fire. There are neurons that respond to specific orientations (**Figure 15.16a**) and neurons that respond to movement across the skin in a specified direction (**Figure 15.16b**; Hyvärinen & Poranen, 1978; also see Bensmaia et al., 2008; Pei et al., 2011; Yau et al., 2009).

There are also neurons in the monkey's somatosensory cortex that respond when the monkey grasps a specific object (Sakata & Iwamura, 1978). For example, **Figure 15.17** shows the response of one of these neurons. This neuron responds when the monkey grasps the ruler but does not respond when the monkey grasps a cylinder or a sphere (see also Iwamura, 1998).

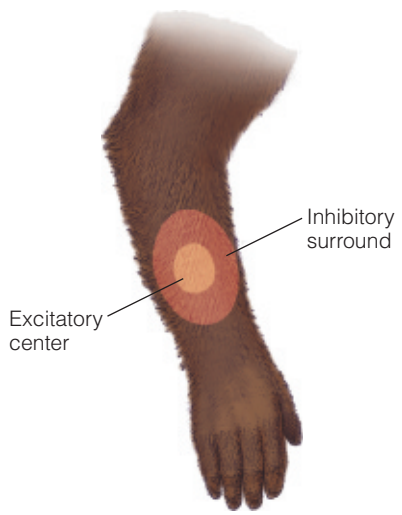

Figure 15.15 An excitatory-center, inhibitory-surround receptive field of a neuron in a monkey's thalamus.

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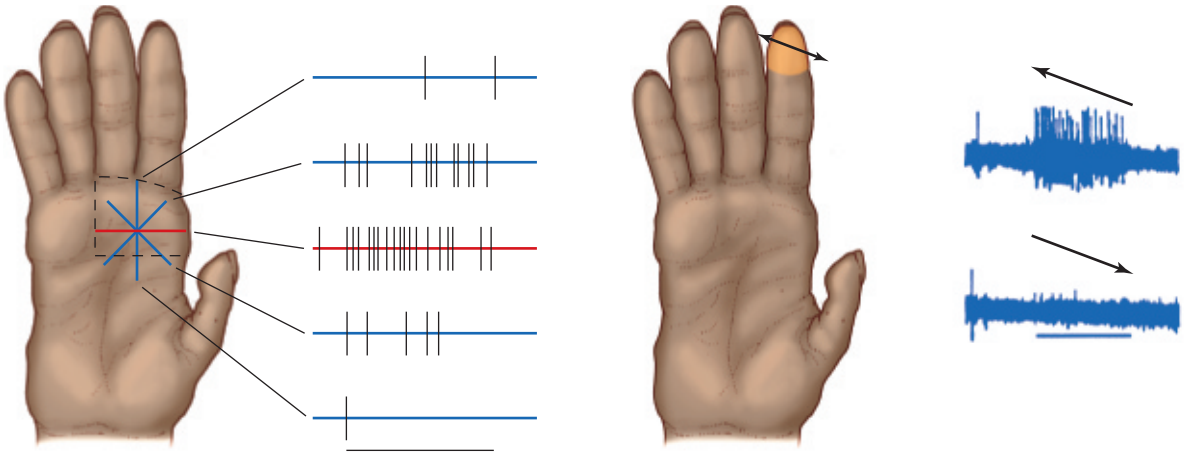

Figure 15.16 Receptive fields of neurons in the monkey's somatosensory cortex. (a) The records to the right of the hand show nerve firing to stimulation of the hand with the orientations shown on the hand. This neuron responds best when a horizontally oriented edge is presented to the monkey's hand. (b) The records on the right indicate nerve firing for movement of a stimulus across the fingertip from right to left (top) and from left to right (bottom). This neuron responds best when a stimulus moves across the fingertip from right to left. (From Hyvärinen & Poranen, 1978)

Cortical Responding Is Affected by Attention

Cortical neurons are affected not only by the properties of an object but also by whether the perceiver is paying attention. Steven Hsiao and coworkers (1993, 1996) recorded the response of neurons in areas S1 and S2 to raised letters that were scanned across a monkey's finger. In the tactile-attention condition, the monkey had to perform a task that required focusing its attention on the letters being presented to its fingers. In the visual-attention condition, the monkey had to focus its attention on an unrelated visual stimulus. The results, shown in **Figure 15.18**, show that even though the monkey is receiving exactly the same stimulation on its fingertips in both conditions, the response is larger for the tactile-attention condition. Thus, stimulation of the receptors may trigger a response, but the size of the response can be affected by processes such as attention, thinking, and other actions of the perceiver.

If the idea that events other than stimulation of the receptors can affect perception sounds familiar, it is because similar situations occur in vision (see pages 133, 164) and hearing (p. 344). A person's active participation makes a difference in perception, not just by influencing what stimuli stimulate the receptors but also by influencing the processing that occurs

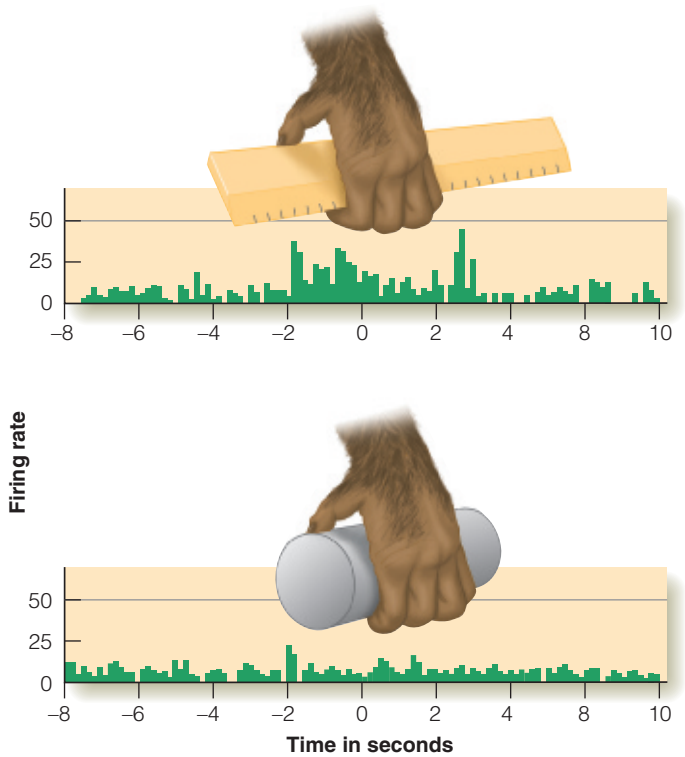

Figure 15.17 The response of a neuron in a monkey's parietal cortex that fires when the monkey grasps a ruler but that does not fire when the monkey grasps a cylinder. The monkey grasps the objects at time = 0. (From Sakata & Iwamura, 1978)

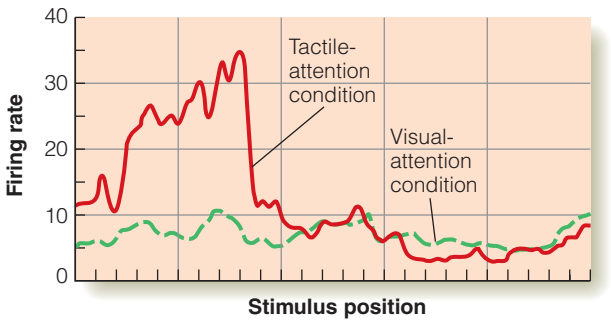

Figure 15.18 Firing rate of a neuron in area S1 of a monkey's cortex to a letter being rolled across the fingertips. The neuron responds only when the monkey is paying attention to the tactile stimulus. (From Hsiao et al., 1993)

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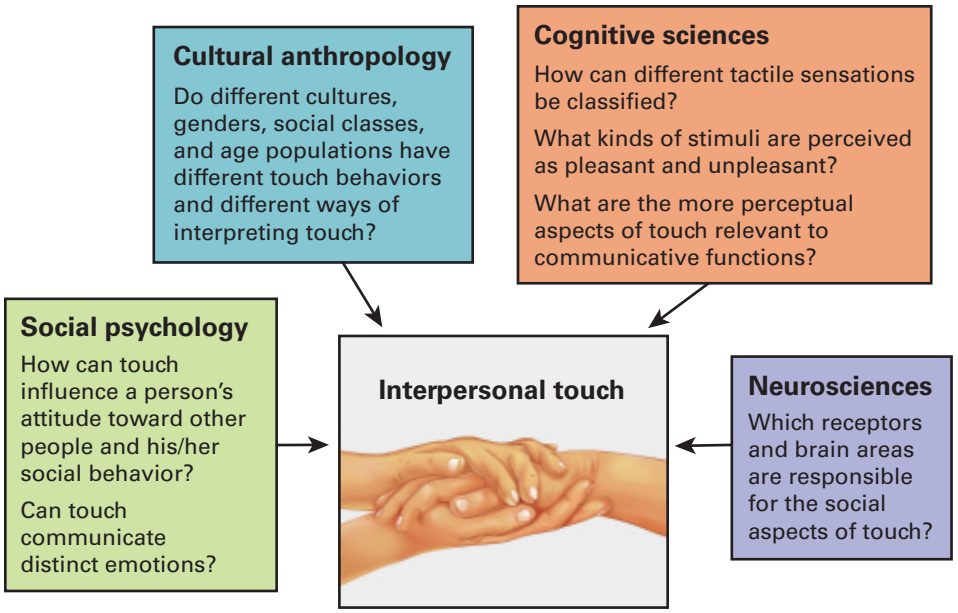
Cultural anthropology
Do different cultures, genders, social classes, and age populations have different touch behaviors and different ways of interpreting touch?
Cognitive sciences
How can different tactile sensations be classified?
What kinds of stimuli are perceived as pleasant and unpleasant?
What are the more perceptual aspects of touch relevant to communicative functions?
Social psychology
How can touch influence a person's attitude toward other people and his/her social behavior?
Can touch communicate distinct emotions?
Interpersonal touch
Neurosciences
Which receptors and brain areas are responsible for the social aspects of touch?

Figure 15.19 The disciplines concerned with research on social touch and some of the questions being posed by each discipline. (Adapted from Gallace & Spence, 2010)

once the receptors are stimulated. Later, we will see that this is clearly demonstrated for the experience of pain, which is strongly affected by processes in addition to stimulation of the receptors.

15.5 Social Touch

What happens when you are touched by another person? One person touching another person, which is called **interpersonal touching** or **social touch**, has recently become a "hot topic" for researchers in a number of different areas (Gallace & Spence, 2010). **Figure 15.19** indicates the kinds of questions that are being asked about social touch. We will focus on the questions in the "cognitive sciences" and "neurosciences" boxes: "What kinds of stimuli are perceived as pleasant and unpleasant?" and "Which receptors and brain areas are responsible for the social aspects of touch?"

Sensing Social Touch

At the beginning of the chapter, we described four types of receptors that occur in glabrous (non-hairy) skin. We now focus on hairy skin, which contains nerve fibers called **CT afferents**, where CT stands for C-tactile. These fibers are unmyelinated, which means that they are not covered by the myelin sheath that covers the fibers associated with the receptors in glabrous skin. Unmyelinated fibers conduct nerve impulses much more slowly than myelinated fibers, a property which we will see is reflected in the type of stimuli they respond to. The activity of these slow-conducting CT fibers was first recorded using a technique called **microneurography**, which involves inserting a metal electrode with a very fine tip just under the skin (**Figure 15.20**) (Vallbo & Hagbarth, 1968; Vallbo et al., 1993).

As recently as 2002, the function of CT afferents was not known. However, Hakan Olausson and coworkers (2002) took a step toward solving this mystery by studying patient G.L., a 54-year-old woman who contracted a disease that destroyed all of her myelinated fibers, which she reported had caused her to lose her sensation of touch. However, careful testing revealed that she could detect light brush strokes presented to the hairy part of her forearm, which contains CT afferents. In addition, her sensations of light touch were accompanied by activation of the *insula*, which we will see receives signals from CT afferents. These results led Olausson to propose that CT afferents are involved in "caress-like skin to skin contact between individuals"—the type of stimulation that came to be called social touch.

The Social Touch Hypothesis

Research that followed the study of G.L. led to the **social touch hypothesis**, which is that CT afferents and their central

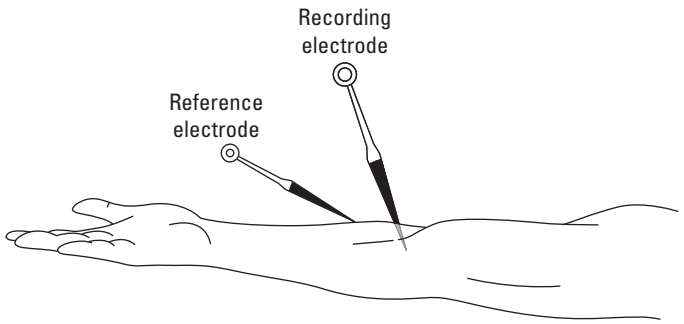

Figure 15.20 Microneurography, which involves inserting mental electrodes with very fine tips just under the skin, has been used to record from cutaneous fibers. When the skin on the forearm is stroked, the electrodes pick up signals as they are transmitted in nerve fibers conducting signals toward the brain.

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projections are responsible for social touch. This was recognized as a new touch system that is different from the systems we described earlier in the chapter, which sense the **discriminative functions of touch**—sensing details, texture, vibration, and objects. The CT system, in contrast, is the basis of the **affective function of touch**—sensing pleasure and therefore often eliciting positive emotions.

Line Loken and coworkers (2009) focused on the pleasant aspect of social touch by using microneurography to record how fibers in the skin responded to stroking the skin with a soft brush. Loken found that the stroking caused firing in CT afferents and also in the SA1 and SA2 myelinated fibers associated with the discriminative functions, but with an important difference. Whereas the response of SA1 and SA2 fibers continued to increase as stroking velocity increased all the way to 30 cm per second (**Figure 15.21a**), the response of the CT afferents peaked at 3–10 cm per second and then decreased (**Figure 15.21b**). CT afferents are therefore specialized for slow stroking. And perhaps as important, Loken also had participants rate the pleasantness of the sensation caused by this slow stroking and found a relationship between pleasantness and CT afferent firing (**Figure 15.21c**). Further research showed that maximum pleasantness ratings occurred at stroking speeds associated with optimal CT firing (Pawling et al., 2017).

Social Touch and the Brain

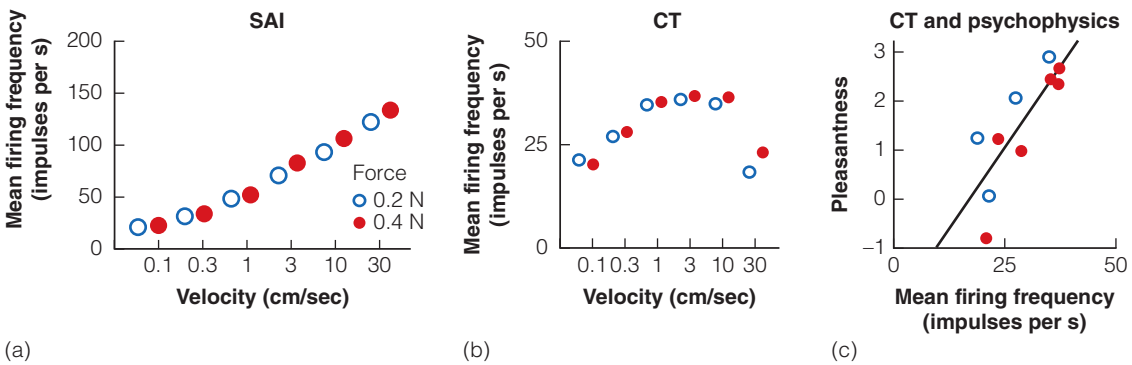
As important as CT afferents are for social touch, the perception of touch doesn't happen until the signals from the CT afferents reach the brain. The main area that receives this input is the insula (see Figure 15.4), which had been known to be involved in positive emotions. Monika Davidovic and coworkers (2019) determined the functional connectivity between different part of the insula caused by pleasant touch (see page 33 to review functional connectivity) and found that slow stroking creates connections between the back of the insula, which receives sensory information, and the front of the insula, which is connected to emotional areas of the brain. Apparently, this connection to emotional areas helps create the pleasurable response to social touch.

Top-Down Influences on Social Touch

The theme of our discussion so far is that slow stroking of the arm (and other parts of the body) is pleasant. But the effects of slow stroking can be influenced by factors in addition to the location and rate of stroking. For example, knowledge of who is doing the stroking can determine whether the stroking is perceived as pleasant or unpleasant.

Dan-Mikael Ellingsen and coworkers (2016) demonstrated this effect by having heterosexual male participants rate the pleasantness on a scale of 1 (very unpleasant) to 20 (very pleasant) of a sensual caress to their arm. They were led to believe that the caress was delivered by a female or a male, and although the stroking was the same in both cases, the pleasantness rating was 9.2 if they thought they were being stroked by a male, and 14.2 if they thought they were being stroked by a female.

Results such as this demonstrate that although slow stroking is often pleasant, evaluation of the situation can turn a pleasant interaction into a less pleasant interaction or even a negative one. The fact that people's thoughts about who is touching them can influence their perception of pleasantness is an example of how **top-down processing** (also called **knowledge-based processing**) (see Chapter 1, page 10) can influence the perception of social touch. When we discuss pain, in the next section, we will describe many examples of how pain can be influenced by top-down processes.



(a) (b) (c)

Figure 15.21 Line Loken and coworkers (2009) used microneurography to record firing rates of (a) SA1 fibers (associated with Merkel receptors) and (b) CT afferents, as a function of the velocity a soft brush was moved across the skin for two different brush pressures, low (blue) and high (red). The firing rate of the SA1 fibers continues to increase as velocity increases, but the firing of the CT afferent peaks at about 3 cm/second and then decreases. (c) The relationship between pleasantness ratings and velocity firing frequency of CT afferents, showing that higher firing rates are associated with higher pleasantness ratings.

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Pain Perception

As we mentioned at the beginning of this chapter, pain functions to warn us of potentially damaging situations and therefore helps us avoid or deal with cuts, burns, and broken bones. People born without the ability to feel pain might become aware that they are leaning on a hot stove burner only when they smell burning flesh, or might be unaware of broken bones, infections, or internal injuries—situations that could easily be life-threatening (Watkins & Maier, 2003). The signaling function of pain is reflected in the following definition, from the International Association for the Study of Pain: "Pain is an unpleasant sensory and emotional experience associated with actual or potential tissue damage, or described in terms of such damage" (Merskey, 1991).

Joachim Scholz and Clifford Woolf (2002) distinguish three different types of pain. **Inflammatory pain** is caused by damage to tissue or inflammation of joints or by tumor cells. **Neuropathic pain** is caused by lesions or other damage to the nervous system. Examples of neuropathic pain are carpal tunnel syndrome, which is caused by repetitive tasks such as typing; spinal cord injury; and brain damage due to stroke.

Nociceptive pain is pain caused by activation of receptors in the skin called **nociceptors**, which are specialized to respond to tissue damage or potential damage (Perl, 2007). A number of different kinds of nociceptors respond to different stimuli—heat, chemical, severe pressure, and cold (**Figure 15.22**). We will focus on nociceptive pain. Our discussion will include not only pain that is caused by stimulation of nociceptors in the skin, but also mechanisms that affect the perception of nociceptive pain, and even some examples of pain that can occur when the skin is not stimulated at all.

15.6 The Gate Control Model of Pain

We begin our discussion of pain by considering how early researchers thought about pain, and how these early ideas began changing in the 1960s. In the 1950s and early 1960s, pain was explained by the **direct pathway model of pain**. According to this model, pain occurs when nociceptor receptors in the skin are stimulated and send their signals directly from the skin to the brain (Melzack & Wall, 1965). But in the 1960s, some researchers began noting situations in which pain was affected by factors in addition to stimulation of the skin.

One example was the report by Beecher (1959) that most American soldiers wounded at the Anzio beachhead in World War II "entirely denied pain from their extensive wounds or had so little that they did not want any medication to relieve it" (p. 165). One reason for this was that the soldiers' wounds had a positive aspect: they provided escape from a hazardous battlefield to the safety of a behind-the-lines hospital.

Another example, in which pain occurs without any transmission from receptor to brain, is the phenomena of **phantom limbs**, in which people who have had a limb amputated continue to experience the limb (**Figure 15.23**). This perception is so convincing that amputees have been known to try stepping off a bed onto phantom feet or legs, or to attempt to lift a cup with a phantom hand. For many, the limb moves with the body, swinging while walking. But perhaps most interesting of all, it is not uncommon for amputees to experience pain in the phantom limb (Jensen & Nikolajsen, 1999; Katz & Gagliese, 1999; Melzack, 1992; Ramachandran & Hirstein, 1998).

One idea about what causes pain in the phantom limb is that signals are sent from the part of the limb that remains after amputation. However, researchers noted that cutting the nerves that used to transmit signals from the limb to the brain does not eliminate either the phantom limb or the pain and concluded that the pain must originate not in the skin but in the brain. In addition, examples such as not perceiving the pain from serious wounds or perceiving pain when no signals are being sent to the brain could not be explained

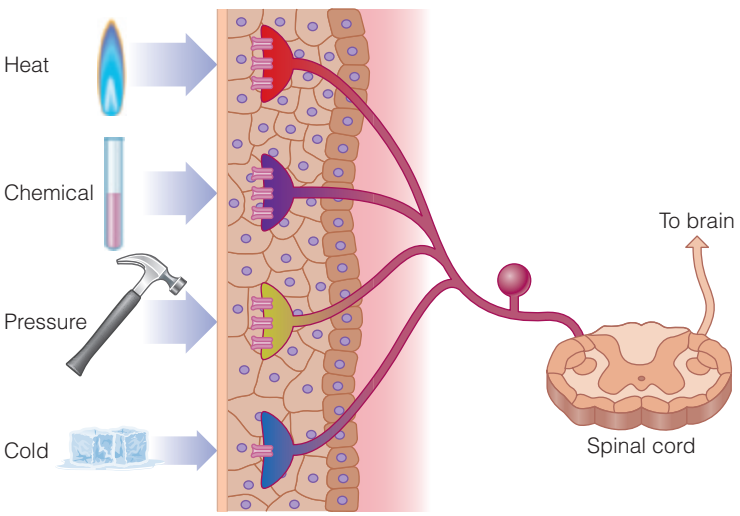

Figure 15.22 Nociceptive pain is created by activation of nociceptors in the skin that respond to different types of stimulation. Signals from the nociceptors are transmitted to the spinal cord and then up the spinal cord in pathways that lead to the brain.

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Figure 15.23 The light part of the right arm represents the phantom limb—an extremity that is not physically present, but which the person perceives as existing.

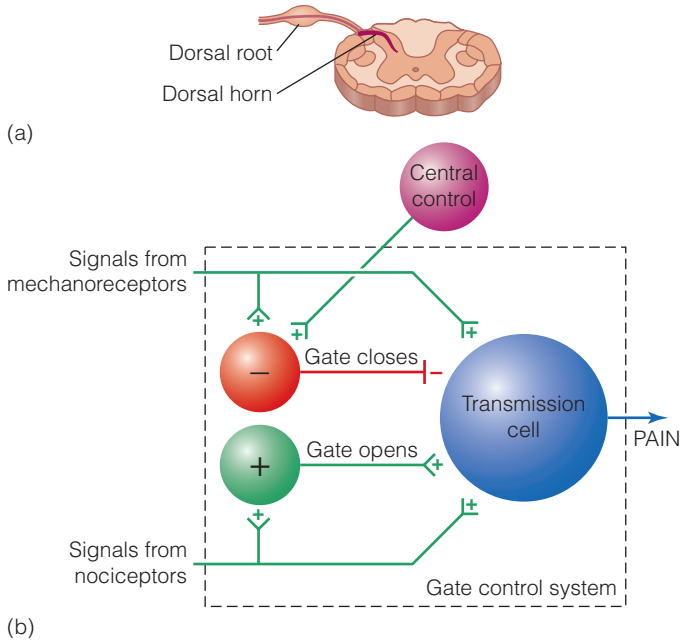

Figure 15.24 (a) Cross section of the spinal cord showing fibers entering through the dorsal root. (b) The circuit proposed by Melzack and Wall (1965, 1988) for their gate control model of pain perception. See text for details.

by the direct pathway model. This led Ronald Melzak and Patrick Wall (1965, 1983, 1988) to propose the *gate control model* of pain.

The gate control model begins with the idea that pain signals enter the spinal cord from the body and are then transmitted from the spinal cord to the brain. In addition, the model proposes that there are additional pathways that influence the signals sent from the spinal cord to the brain. The central idea behind the theory is that signals from these additional pathways can act to open or close a *gate*, located in the spinal cord, which determines the strength of the signal leaving the spinal cord.

Figure 15.24 shows the circuit that Melzack and Wall (1965) proposed. The gate control system consists of cells in the dorsal horn of the spinal cord (**Figure 15.24a**). These cells in the dorsal horn are represented by the red and green circles in the gate control circuit in **Figure 15.24b**. We can understand how this circuit functions by considering how input to the gate control system occurs along three pathways:

- *Nociceptors*. Fibers from nociceptors activate a circuit consisting entirely of excitatory synapses, and therefore send excitatory signals to the transmission cells. Excitatory signals from the (+) neurons in the dorsal horn "open the gate" and increase the firing of the transmission cells. Increased activity in the transmission cells results in more pain.
- *Mechanoreceptors*. Fibers from mechanoreceptors carry information about nonpainful tactile stimulation. An example of this type of stimulus would be signals sent from rubbing the skin. When activity in the mechanoreceptors reaches the (–) neurons in the dorsal horn, inhibitory signals sent to the transmission cells "close the gate" and decrease the firing of the transmission cells. This decrease in firing decreases the intensity of pain.
- *Central control*. These fibers, which contain information related to cognitive functions such as expectation, attention, and distraction, carry signals down from the cortex. As with the mechanoreceptors, activity coming down from the brain also closes the gate, decreases transmission cell activity, and decreases pain.

Since the introduction of the gate control model in 1965, researchers have determined that the neural circuits that control pain are much more complex than what was proposed in the original model (Perl & Kruger, 1996; Sufka & Price, 2002). Nonetheless, the idea proposed by the model—that the perception of pain is determined by a balance between input from nociceptors in the skin and nonnociceptive activity from the skin and the brain—stimulated research that provided a great deal of additional evidence for the idea that the perception of pain is influenced by more than just stimulation of the skin (Fields & Basbaum, 1999; Sufka & Price, 2002; Turk & Flor, 1999; Weissberg, 1999). We will now consider some examples of how cognition can influence the perception of pain.

15.7 Top-Down Processes

Modern research has shown that pain can be influenced by what a person expects, how the person directs his or her attention, the type of distracting stimuli that are present, and suggestions made under hypnosis (Rainville et al., 1999; Wiech et al., 2008).

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Expectation

In a hospital study in which surgical patients were told what to expect and were instructed to relax to alleviate their pain, the patients requested fewer painkillers following surgery and were sent home 2.7 days earlier than patients who were not provided with this information (Egbert et al., 1964). Studies have also shown that a significant proportion of patients with pathological pain get relief from taking a **placebo**, a pill that they believe contains painkillers but that, in fact, contains no active ingredients (Finniss & Benedetti, 2005; Weisenberg, 1977). This decrease in pain from a substance that has no pharmacological effect is called the **placebo effect**. The key to the placebo effect is that the patient believes that the substance is an effective therapy. This belief leads the patient to expect a reduction in pain, and this reduction does, in fact, occur. Many experiments have shown that expectation is one of the more powerful determinants of the placebo effect (Colloca & Benedetti, 2005).

Ulrike Bingel and coworkers (2011) demonstrated the effect of expectation on painful heat stimulation presented by an electrode on the calf of a person's leg. The heat was adjusted so the participant reported a pain rating of 70, where 0 corresponds to "no pain," and 100 to "unbearable pain." Participants then rated the pain in a condition in which a saline solution was presented by infusion (*baseline*) and three conditions in which the analgesic drug remifentanil was presented, but the participants were told (1) that they were still receiving the saline solution (*no expectation*); (2) that the drug was being presented (*positive expectation*); and (3) that the drug was going to be discontinued in order to investigate the possible increase in pain that would occur (*negative expectation*).

The results, shown in **Table 15.2**, indicate that pain was reduced slightly, from 66 to 65, in the no expectation condition when the drug infusion began, but dropped to 39 in the positive expectation condition, then increased to 64 in the negative expectation condition. The important thing about these results is that after the saline baseline condition, the participant was continuously receiving the same dose of the drug. What was being changed was their expectation, and this change in expectation changed their experience of pain.

The decrease in pain experienced in the positive expectation condition is a placebo effect, in which the positive expectation instructions function as the placebo. Conversely, the negative effect caused by the negative expectation instructions is called a **nocebo effect**, a negative placebo effect (see Tracey, 2010, for a review of placebo and nocebo effects).

This study also measured the participants' brain activity and found that the placebo effect was associated with increases in a network of areas associated with pain perception, and the nocebo effect was associated with increases in activity in the hippocampus. A person's expectation therefore affects both perception and physiological responding.

Table 15.2 Effect of Expectation on Pain Ratings

CONDITION	DRUG?	PAIN RATING
Baseline	No	66
No expectation	Yes	55
Positive expectation	Yes	39
Negative expectation	Yes	64

Source: Bingel et al., 2011.

Attention

When we described perceiving textures by the fingers, we saw that the response of cortical neurons can be influenced by attention (Figure 15.18). Similar effects occur for pain perception. Examples of the effect of attention on pain were noted in the 1960s by Melzack and Wall (1965) as they were developing their gate control theory of pain. Here is a recent description of this effect, as reported by a student in my class:

> I remember being around five or six years old, and I was playing Nintendo when my dog ran by and pulled the wire out of the game system. When I got up to plug the wire back in I stumbled and banged my forehead on the radiator underneath the living room window. I got back up and staggered over to the Nintendo and plugged the controller back into the port, thinking nothing of my little fall. ... As I resumed playing the game, all of a sudden I felt liquid rolling down my forehead, and reached my hand up to realize it was blood. I turned and looked into the mirror on the closet door to see a gash running down my forehead with blood pouring from it. All of a sudden I screamed out, and the pain hit me. My mom came running in, and took me to the hospital to get stitches. (Ian Kalinowski)

The important message of this description is that Ian's pain occurred not when he was injured but when he *realized* he was injured. One conclusion that we might draw from this example is that one way to decrease pain would be to distract a person's attention from the source of the pain. This technique has been used in hospitals with virtual reality techniques as a tool to distract attention from a painful stimulus. Consider, for example, the case of James Pokorny, who received third-degree burns over 42 percent of his body when the fuel tank of the car he was repairing exploded. While having his bandages changed at the University of Washington Burn Center, he wore a black plastic helmet with a computer monitor inside, on which he saw a virtual world of multicolored three-dimensional graphics. This world placed him in a virtual kitchen that contained a virtual spider, and he was able to chase the spider into the sink so he could grind it up with a virtual garbage disposal (Robbins, 2000).

The point of this "game" was to reduce Pokorny's pain by shifting his attention from the bandages to the virtual reality world. Pokorny reports that "you're concentrating on different things, rather than your pain. The pain level went down

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significantly." Studies of other patients indicate that burn patients using this virtual reality technique experienced much less pain when their bandages were being changed than patients in a control group who were distracted by playing video games (Hoffman et al., 2000) or who were not distracted at all (Hoffman et al., 2008; also see Buhle et al., 2012).

Emotions

A great deal of evidence shows that pain perception can be influenced by a person's emotional state, with many experiments showing that positive emotions are associated with decreased pain (Bushnell et al., 2013). Two ways this has been demonstrated is by having people look at pictures and having them listen to music.

Minet deWied and Marinis Verbaten (2001) had participants look at pictures that had been previously rated as being positive (sports pictures and attractive females), neutral (household objects, nature, and people), or negative (burn victims and accidents). The participants looked at the pictures while one of their hands was immersed in cold (2°C/35.6°F) water, and they were told to keep the hand immersed for as long as possible but to withdraw the hand when it began to hurt.

The results indicated that participants who were looking at the positive pictures kept their hands immersed for an average of 120 seconds, but participants in the other groups removed their hands more quickly (80 seconds for neutral pictures; 70 seconds for negative pictures). Because their ratings of the intensity of their pain—made immediately after removing their hands from the water—was the same for all three groups, deWied and Verbaten concluded that the content of the pictures influenced the time it took to reach the same pain level in the three groups. In another experiment, Jaimie Rhudy and coworkers (2005) found that participants gave lower ratings to pain caused by an electric shock when they were looking at pleasant pictures than when they were looking at unpleasant pictures. They concluded from this result that positive or negative emotions can affect the experience of pain.

Music is another way to elicit emotions, both positive and negative (Altenmüller et al., 2014; Fritz et al., 2009; Koelsch, 2014). These emotional effects are one of the primary reasons we listen to music, but there is also evidence that the positive emotions associated with music can decrease pain. Mathieu Roy and coworkers (2008) measured how music affected the perception of a thermal heat stimulus presented to the forearm by having participants rate the intensity and unpleasantness of the pain on a scale of 0 (no pain) to 100 (extremely intense or extremely unpleasant), under one of these three conditions: listening to unpleasant music (example: Sonic Youth, *Pendulum Music*), listening to pleasant music (example: Rossini, *William Tell Overture*), and silence.

The results of Roy's experiment for the highest temperature used (48°C/119°F), shown in **Table 15.3**, indicates that listening to unpleasant music didn't affect pain, compared to silence, but that listening to pleasant music decreased both the intensity and the unpleasantness of pain. In fact, the pain relief caused by the pleasant music was comparable to the effects of common analgesic drugs such as ibuprofen.

Table 15.3 Effect of Pleasant and Unpleasant Music on Pain

CONDITION	INTENSITY RATING	UNPLEASANTNESS RATING
Silence	69.7	60.0
Unpleasant music	68.6	60.1
Pleasant music	**57.7**	**47.8**

Source: Roy et al., 2008.

TEST YOURSELF 15.2

1. What processes are involved in identifying objects by haptic exploration?
2. Describe the specialization of cortical areas for touch and how cortical responding to touch is affected by attention.
3. What is social touch?
4. Which receptors in the skin are responsible for social touch?
5. What is the social touch hypothesis?
6. What brain areas are involved in social touch?
7. How do "situational influences" affect social touch?
8. Describe the three types of pain.
9. What is the direct pathway model of pain? What evidence led researchers to question this model of pain perception?
10. What is the gate control model? Be sure you understand the roles of the nociceptors, mechanoreceptors, and central control.
11. Describe evidence that supports the conclusions that pain is influenced by expectation, attention, and emotion.

15.8 The Brain and Pain

Research on the physiology of pain has focused on identifying areas of the brain and the chemicals that are involved in pain perception.

Brain Areas

A large number of studies support the idea that the perception of pain is accompanied by activity that is widely distributed throughout the brain. **Figure 15.25** shows a number of the structures that become activated by pain. They include subcortical structures, such as the hypothalamus, the amygdala, and the thalamus, and areas in the cortex, including

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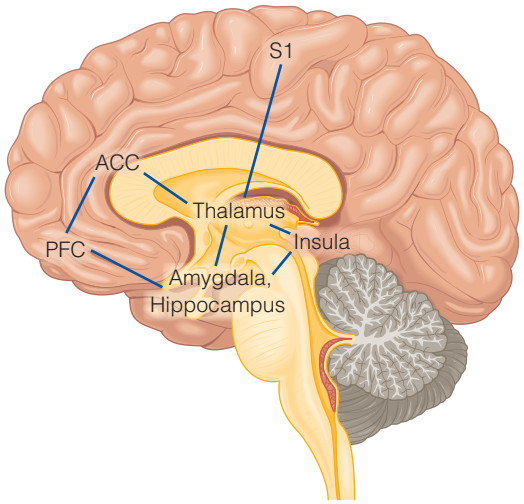

Figure 15.25 The perception of pain is accompanied by activation of a number of different areas of the brain. ACC is the anterior cingulate cortex; PFC is the prefrontal cortex; S1 is the somatosensory cortex. The positions of the structures are approximate, with some, such as the amygdala, hypothalamus, and insula, located deep within the cortex, and others, such as S1 and PFC, located at the surface. Lines indicate connections between the structures.

the somatosensory cortex (S1), the anterior cingulate cortex (ACC), the prefrontal cortex (PFC), and the insula (Chapman, 1995; Derbyshire et al., 1997; Price, 2000; Rainville, 2002; Tracey, 2010). Although pain is associated with the overall pattern of firing in the many structures, there is also evidence that certain areas are responsible for specific components of the pain experience.

In the definition of pain on page 373, we stated that pain is "an unpleasant sensory and emotional experience." This reference to both sensory *and* emotional experience reflects the **multimodal nature of pain**, which is illustrated by how people describe pain. When people describe their pain with words like *throbbing*, *prickly*, *hot*, or *dull*, they are referring to the **sensory component of pain**. When they use words like *torturing*, *annoying*, *frightful*, or *sickening*, they are referring to the **affective** (or **emotional**) **component of pain** (Melzack, 1999).

The sensory and affective components of pain can be distinguished by asking participants who are experiencing painful stimuli to rate subjective pain intensity (sensory component) and unpleasantness (affective component), as was done in the music study described in the previous section. When R. K. Hofbauer and coworkers (2001) used hypnotic suggestion to increase or decrease these components separately, they found that changes in the sensory component were associated with activity in the somatosensory cortex and changes in the affective component were associated with changes in the anterior cingulate cortex. **Figure 15.26** shows these two areas and some other areas that have been determined from other experiments to be associated with sensory (blue) and affective (green) pain experiences (Eisenberger, 2015).

Chemicals and the Brain

Another important development in our understanding of the relationship between brain activity and pain perception is the discovery of a link between chemicals called **opioids** and pain perception. This can be traced back to research that began in the 1970s on opiate drugs, such as opium and heroin, which have been used since the dawn of recorded history to reduce pain and induce feelings of euphoria.

By the 1970s, researchers had discovered that opiate drugs act on receptors in the brain that respond to stimulation by molecules with specific structures. The importance of the molecule's structure for exciting these "opiate receptors" explains why injecting a drug called **naloxone** into a person who has overdosed on heroin can almost immediately revive the victim. Because naloxone's structure is similar to heroin's, it attaches to the same receptor sites, thereby preventing from binding to those receptors (**Figure 15.27a**).

Why are there opiate receptor sites in the brain? After all, they certainly have been present since long before people started taking heroin. Researchers concluded that there must be naturally occurring substances in the body that act on these sites, and in 1975 neurotransmitters were discovered that act on the same receptors that are activated by opium and heroin. One group of these transmitters is called **endorphins**, for *endogenous* (naturally occurring) *morphine*.

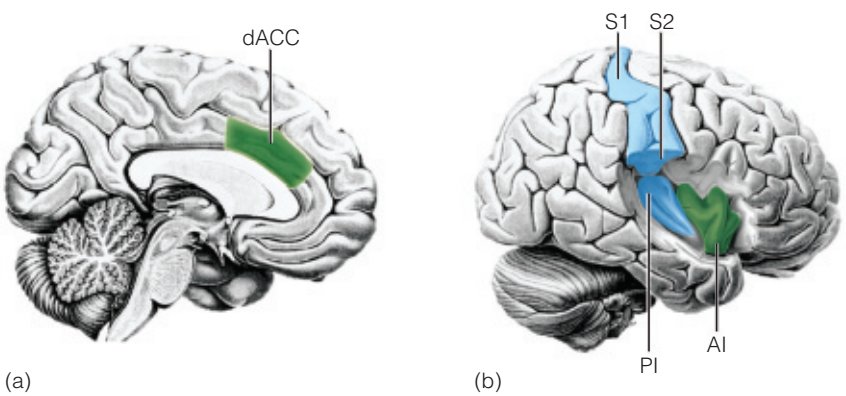

Figure 15.26 Two views of the brain showing the areas involved in the affective and sensory components of pain. Green = Affective component: ACC = anterior cingulate cortex; AI = anterior insula; Blue = Sensory component: S1, S2 = somatosensory areas; PI = posterior insula. (Adapted from Eisenberger, 2015, Fig 1, p. 605)

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Since the discovery of endorphins, researchers have accumulated a large amount of evidence linking endorphins to pain reduction. For example, pain can be decreased by stimulating sites in the brain that release endorphins (**Figure 15.27b**), and pain can be increased by injecting naloxone, which blocks endorphins from reaching their receptor sites (**Figure 15.27c**).

In addition to decreasing the analgesic effect of endorphins, naloxone also decreases the analgesic effect of placebos (see page 375). This finding, along with other evidence, led to the conclusion that the pain reduction effect of placebos occurs because placebos cause the release of endorphins. As it turns out, there are some situations in which the placebo effect can occur without the release of endorphins, but we will focus on the endorphin-based placebo effect by considering the following question, raised by Fabrizio Benedetti and coworkers (1999): Where are placebo-related endorphins released in the nervous system?

Benedetti wondered whether expectation caused by placebos triggered the release of endorphins throughout the brain, therefore creating a placebo effect for the entire body, or whether expectation caused the release of endorphins only at specific places in the body. To answer this question, Benedetti injected participants with the chemical *capsaicin* just under the skin at four places on the body: the left hand, the right hand, the left foot, and the right foot. Capsaicin, which is the active component in chili peppers, causes a burning sensation where it is injected.

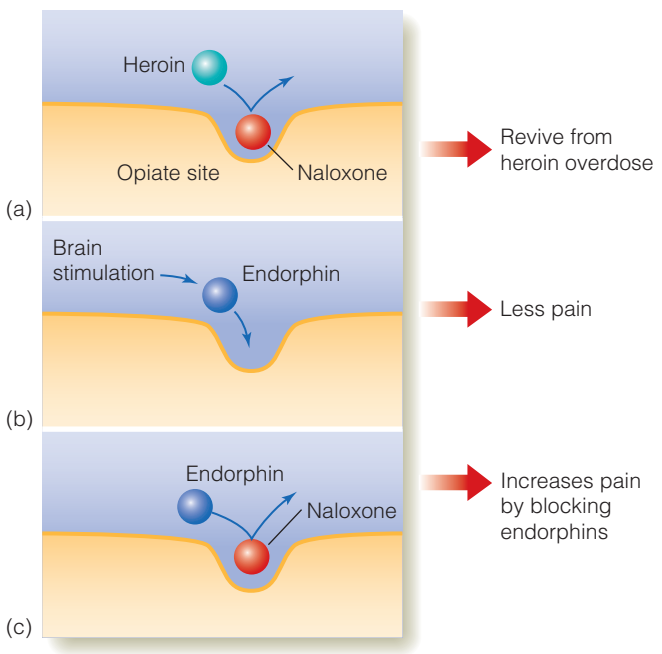

Figure 15.27 (a) Naloxone, which has a structure similar to heroin, reduces the effect of heroin by occupying a receptor site normally stimulated by heroin. (b) Stimulating sites in the brain that cause the release of endorphins can reduce pain by stimulating opiate receptor sites. (c) Naloxone decreases the pain reduction caused by endorphins by keeping the endorphins from reaching the receptor sites.

Table 15.4 Effect of Placebo Cream on Different Parts of the Body

	PAIN RATINGS AT DIFFERENT BODY LOCATIONS			
CONDITION	LEFT HAND	RIGHT HAND	LEFT FOOT	RIGHT FOOT
No placebo	6.6	5.5	6.0	5.4
Placebo cream on left hand	**3.0**	6.4	5.3	6.0
Placebo cream on right hand and left foot	5.4	**3.0**	**3.8**	6.3

Source: Benedetti et al., 1999.

One group of participants rated the pain at each part of the body on a scale of 0 (no pain) to 10 (unbearable pain) every minute for 15 minutes after the injection. The "No placebo" row in **Table 15.4** shows that the participants in this group reported pain at all the locations (ratings between 5.4 and 6.6). Another group of participants also received the injection, but just before the injections, the experimenter rubbed a cream at one or two of the locations and told participants that the cream was a potent local anesthetic that would relieve the burning sensation of the capsaicin. The cream was actually a placebo treatment; it had no pain-reducing ingredients.

The second row of Table 15.4 shows that the pain rating for the left hand decreased to 3.0 for a participant who received the cream on the left hand, and the third row shows that the pain ratings for the right and left foot decreased for a participant who received the cream on the right hand and left foot. These results are striking because the placebo effect occurred only where the cream was applied. To demonstrate that this placebo effect was associated with endorphins, Benedetti showed that injecting naloxone abolished the placebo effect.

What this means, according to Benedetti, is that when participants direct their attention to specific places where they expect pain will be reduced, pathways are activated that release endorphins at specific locations. The mechanism behind endorphin-related analgesia is therefore much more sophisticated than simply chemicals being released into the overall circulation. The mind, as it turns out, can not only reduce pain by causing the release of chemicals, it can literally direct these chemicals to the locations where the pain would be occurring. Research such as this, which links the placebo effect to endorphins, provides a physiological basis for what had previously been described in strictly psychological terms.

15.9 Social Aspects of Pain

We've described social aspects of touch, in which activation of CT afferents is associated with the pleasurable sensation that often accompanies slow stroking of the skin. In this section we will describe three connections between "social" and pain: (1) how social touch can reduce pain; (2) how observing someone else feeling pain can affect the observer; and (3) possible connections between the pain of social rejection and physical pain.

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Pain Reduction by Social Touch

We've seen that being a recipient of social touch is often perceived as pleasant (p. 372). We now describe an experiment by Pascal Goldstein and coworkers (2018) that was inspired by Goldstein's observation that holding his wife's hand during the delivery of his daughter decreased his wife's pain. **Figure 15.28** shows the position of the two participants in the experiment that studied this observation in the laboratory.

Romantically involved couples wore electrode arrays on their heads to record electroencephalogram (EEG), which is the response of thousands of neurons under the electrodes. They faced each other, but were not allowed to talk to each other. The woman received a heat stimulus on her arm that was moderately painful and was instructed to rate her pain level just before the heat was turned off. On no-touch trials, the man and woman just looked at each other without touching; on touch trials, the man held the woman's hand. There were also trials in which the man was absent.

The results showed that the woman's pain ratings were lower when her partner was holding her hand (rating = 25.0), compared to when he wasn't (37.8) or when he was absent (52.4). This decrease in pain in the hand-holding condition replicates Goldstein's wife's experience in the delivery room. But comparing the woman's and man's EEG responses revealed something that wasn't obvious in the delivery room. The woman's and man's brains were strongly "coupled" or synchronized when holding hands (**Figure 15.29a**), but were not as synchronized when not holding hands (**Figure 15.29b**). The authors suggest that the support provided by hand holding causes synchronized brain waves, which are translated into reduced pain. In addition to this synchronization effect, other research has shown that hand holding reduces activity in brain areas associated with pain (Lopez-Sola et al., 2019). These experiments have two important messages: Providing support by being there for someone who is experiencing pain can reduce their pain, and making physical contact by holding hands reduces the pain even further.

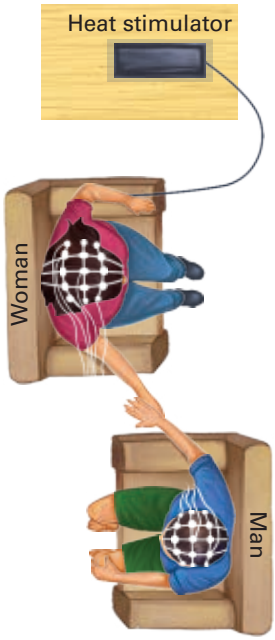

Figure 15.28 Setup for the Goldstein et al. (2018) experiment. See text for details.

The Effect of Observing Someone Else's Pain

Goldstein's experiment demonstrated that holding someone's hand can reduce their pain. This has been described as effect of **empathy**, the ability to share and vicariously experience someone else's feeling. In the hand-holding experiment, the person *receiving* the empathy experienced pain analgesia. We can also look at empathy from another point of view, by considering what is happening for the "empathizer," the person who is *feeling empathy* for the person who is in pain.

In Chapter 7 we introduced the idea that observing an action can cause activity related to that action in the observer's brain. This was demonstrated in experiments studying mirror neurons in the monkey's premotor cortex, which fired both when the monkey picking up an object, such as food, and also when the monkey saw someone else picking up the food.

Research on the somatosensory system has revealed similar phenomena. To introduce this phenomenon, let's first consider an experiment involving touch. Keysers and coworkers (2004) measured the fMRI response of a person's cortex to being touched on the leg. They also measured the

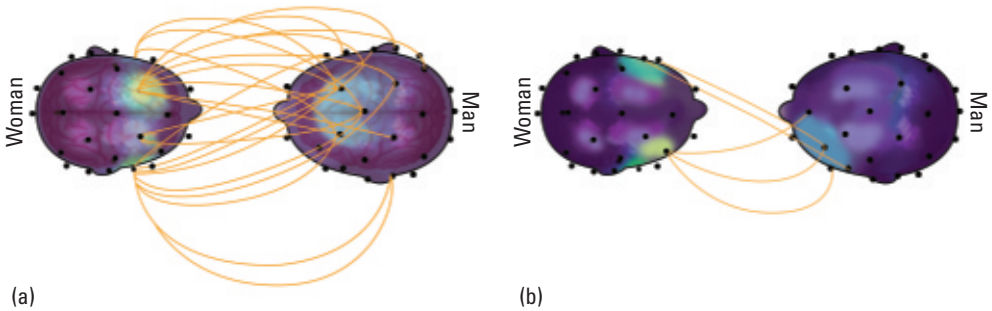

Figure 15.29 Coupling between EEG brain waves of the woman and man when the woman was experiencing pain in the Goldstein et al. (2018) experiment. The orange lines represent synchronized responses between two brain areas. (a) Holding-hands condition. (b) Not holding-hands condition.

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response that occurred when that person viewed a film of another person being touched on the leg. Being touched caused a response in the person's primary somatosensory area (S1) and secondary somatosensory area (S2). Watching someone else being touched caused a response in S2, part of which overlapped with the response to being touched. Keysers concluded from the overlap in the areas that the brain transforms watching someone being touched into an activation of brain areas involved in our own experience of touch (see also Keysers et al., 2010).

Another way to describe Keysers's results is, when we witness someone else being touched, we don't just *see* touch, but we have an empathic response in which we understand the other person's response to touch through a link with *our own experience* of touch. This idea that observing someone else being touched triggers brain mechanisms that might help us understand the other person's response to touch is important because there is also evidence that similar mechanisms operate for pain.

Tania Singer and coworkers (2004) demonstrated the connection between brain responses to pain and empathy by bringing romantically involved couples into the laboratory and having the woman, whose brain activity was being measured by an fMRI scanner, either receive shocks herself or watch her male partner receive shocks. The results, shown in **Figure 15.30**, show that a number of brain areas were activated when the woman received the shocks (**Figure 15.30a**), and that some of the same areas were activated when she watched her partner receive shocks (**Figure 15.30b**). The main two areas activated in common were the anterior cingulate cortex (ACC) and the anterior insula (AI), both of which are associated with the affective component of pain (see Figure 15.26).

To show that the brain activity caused by watching their partner was related to empathy, Singer had the women fill out "empathy scales" designed to measure their tendency to empathize with others. As predicted, women with higher empathy scores showed higher activation of their ACC.

In another experiment, Olga Klimecki and coworkers (2014) had participants undergo training designed to increase their empathy for others and then showed them videos depicting other people experiencing suffering due to injury or natural disasters. Participants in the empathy-training group showed more empathy compared to a control group that hadn't received the training *and* greater activation of the ACC. Thus, although the pain associated with watching someone else experience pain may be caused by stimulation that is very different from physical pain, these two types of pain apparently share some physiological mechanisms. (Also see Avenanti et al., 2005; Lamm et al., 2007; Singer & Klimecki, 2014.)

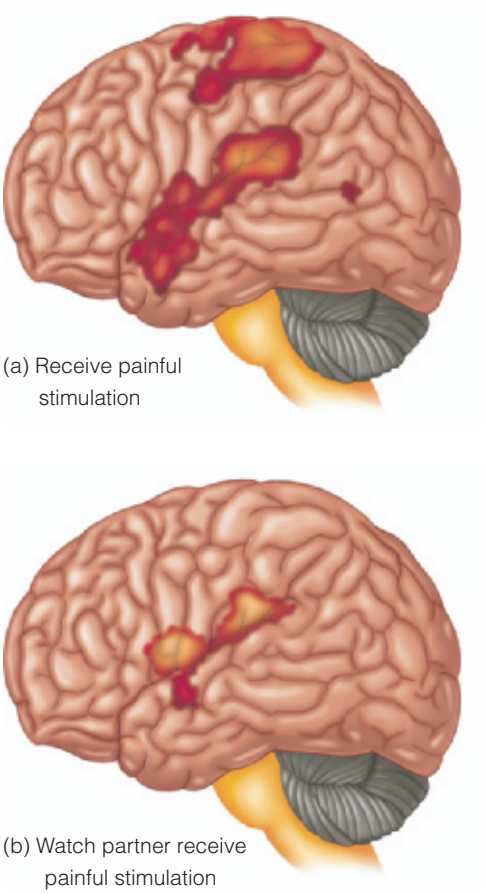

Figure 15.30 Singer and coworkers (2004) used fMRI to determine the areas of the brain activated by (a) receiving painful stimulation and (b) watching another person receive the painful stimulation. Singer proposes that the activation in (b) is related to empathy for the other person. Empathy did not activate the somatosensory cortex but did activate other areas that are activated by pain, such as the insula (tucked between the parietal and temporal lobes) and anterior cingulate cortex (see Figures 15.25 and 15.26). (Adapted from Holden, 2004)

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The "Pain" of Social Rejection

Our discussion of the connection between "social" and "pain" has so far considered effects associated with physical pain—pain caused by heating or shocking the skin. We will now describe something very different—the pain caused by social situations such as social rejection. The question we will be considering is, "What does this **social pain**—pain caused by social interactions—have in common with physical pain?"

The idea that social rejection hurts is well known. When describing emotional responses to negative social experiences, it is common for people to use words associated with physical pain, such as *broken* hearts, *hurt* feelings, or emotional *scars* (Eisenberger, 2012, 2015). In 2003, Naomi Eisenberger and coworkers published a paper titled "Does Rejection Hurt? An fMRI Study of Social Exclusion," which concluded that the dorsal anterior cingulate cortex (dACC; see Figure 15.26) is activated by feelings of social exclusion. They demonstrated this by having participants participate in a video game called "Cyberball," in which they were told that they would be playing a ball-tossing game with two other participants, who were indicated by the two figures at the top of the computer screen, with the participant being indicated by a hand at the bottom of the screen (**Figure 15.31**).

Initially, the two other players included the participant in their ball tossing (**Figure 15.31a**), but then they suddenly excluded the participant and just tossed the ball between themselves (**Figure 15.31b**). This exclusion caused activity in the participant's dACC, as shown in **Figure 15.31c**, and this dACC activity was related to the degree of social distress the participant reported feeling, with greater distress associated with greater dACC activity (**Figure 15.31d**).

Other studies provided more evidence for similar physiological responses to negative social experiences and physical pain. Activation of the dACC and anterior insula (AI) occurred in response to a threat of negative social evaluation (Eisenberger et al., 2011) and when remembering a romantic partner who had recently rejected the person (Kross et al., 2011). Also, taking a pain reliever such as Tylenol not only reduces physical pain but also reduces hurt feelings and dACC and AI activity (DeWall et al., 2010).

Results such as these have led to the **physical-social pain overlap hypothesis**, which proposes that pain resulting from negative social experiences is processed by some of the same neural circuitry that processes physical pain (Eisenberger, 2012, 2015; Eisenberger & Lieberman, 2004). This idea has not gone unchallenged, however. One line of

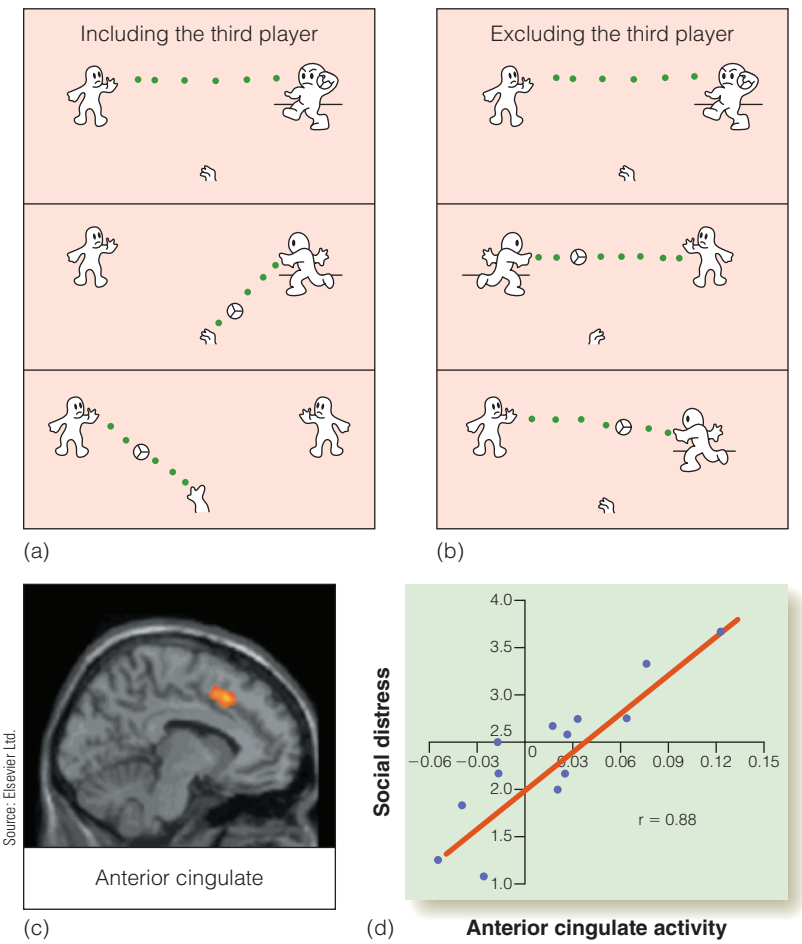

Figure 15.31 The "Cyberball" experiment. (a) The participant is told that the two characters shown on the top of the screen are being controlled by two other participants. These two characters throw the ball to the participant in the first part of the experiment. (b) The participant is excluded from the game in the second part of the experiment. (c) Exclusion results in activity in the ACC, shown in orange. (d) Participant's rating of social distress (y-axis) is related to ACC activation (x-axis). (From Eisenberger & Lieberman, 2004)

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criticism has focused on the idea that activity in the ACC may be reflecting things other than pain. For example, it has been suggested that the ACC may respond to many types of emotional and cognitive tasks, rather than being specialized for pain (Krishnan et al., 2016; Wager et al., 2016), or that the ACC responds to salience—how much a stimulus stands out from its surroundings (Iannetti et al., 2013).

Another question that has been raised is whether activation of the ACC by both social and physical pain means that the same neural circuits are being activated. This question is similar to a question we considered in Chapter 13, when we considered whether music and language share neural mechanisms. One of the points made in that discussion, which is also relevant here, is that just because two functions activate the same area of the brain, doesn't mean that the two functions are activating the same neurons within that area. Look back at Figure 13.24 for an illustration of the idea that activation within a particular area can involve different neural networks.

Choong-Wan Woo and coworkers (2014) used a technique called *multivoxel pattern analysis (MVPA)* to look at what is happening inside the brain structures involved in social and physical pain. MVPA was used for the *neural mind reading* experiment described in Chapter 5 in which the pattern of voxel responses to oriented lines was determined to create computer image decoders for visual stimuli (see Method: Neural Mind Reading, page 114). Woo found that the pattern of voxel responses generated by recalling social rejection by a romantic partner was different from the pattern generated by painful heat presented to the forearm, which why his paper is titled "Separate Neural Representations for Physical Pain and Social Rejection."

So which idea is correct? Do social pain and physical pain share neural mechanisms, or are they two separate phenomena that both use the word "pain"? There is evidence supporting the physical-social pain overlap hypothesis, but there is also evidence that argues against this hypothesis. Because social pain and physical pain are certainly different—it's easy to tell the difference between the feeling of being rejected and the feeling from burning your finger—it is unlikely that mechanisms overlap completely. The physical-social pain overlap hypothesis proposes that there is *some* overlap. But how much is "some"? A little or a lot? Research to answer this question is continuing.

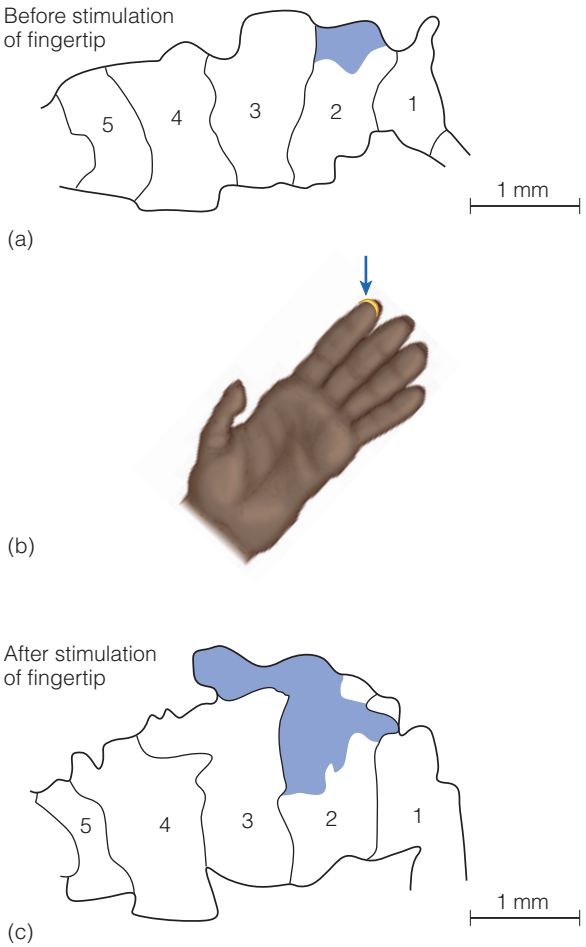

Figure 15.32 (a) Each numbered zone represents the area in the somatosensory cortex that corresponds to one of a monkey's five fingers. The shaded area on the zone for finger 2 is the part of the cortex that represents the small area on the tip of the finger shown in (b). (c) The shaded region shows how the area representing the fingertip increased in size after this area was heavily stimulated over a three-month period. (From Merzenich et al., 1988)

SOMETHING TO CONSIDER:

Plasticity and the Brain

We've seen that there are orderly maps of the body on the somatosensory cortex, in which parts of the body that are more sensitive and are used more, like the lips, hands, and fingers, are represented by large areas on the brain (Figure 15.5).

But these maps can change based both on how much a body part is used and in response to injury. An early study showing that the map changes with use was done by William Jenkins and Michael Merzenich (1987), who began by measuring the cortical areas devoted to each of a monkey's fingers (**Figure 15.32a**). They gave the monkey a task that heavily stimulated the tip of finger 2 over a three-month period (**Figure 15.32b**) and then remeasured the areas devoted to the fingers (**Figure 15.32c**). Comparison of the "before" and "after" cortical maps showed that the area representing the stimulated fingertip was greatly expanded after the training.

This change in the brain's map is an example of *experience-dependent plasticity*, introduced in Chapter 4, when we saw that raising a kitten in an environment consisting only of vertically oriented stripes caused the cat's orientation-sensitive neurons to respond mainly to verticals (p. 74). An effect of experience-dependent plasticity has been demonstrated in humans by measuring the brain maps of musicians. Consider, for example, players of stringed instruments. A right-handed violin player bows with the right hand and uses the fingers

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of his or her left hand to finger the strings. One result of this tactile experience is that these musicians have a greater than normal cortical representation for the fingers on their left hand (Elbert et al., 1995). Just as in the monkeys, plasticity has created more cortical area for parts of the body that are used more.

Changes in the cortical map can also occur when part of the body is damaged. For example, when a monkey loses a finger, the brain area representing that finger no longer receives input from that finger, so over a period of time that area is taken over by the fingers next to the one that is missing (Byl et al., 1996).

A particularly interesting example of a possible change in mapping associated with dysfunction is the case of world-famous concert pianist Leon Fleisher, who, at the age of 36, began experiencing **hand dystonia**, a condition which caused the fingers on his right hand to curl into his palm, making it impossible to play the piano with his right hand. Fleisher developed a repertoire of left-handed piano compositions, and eventually, after 30 years of therapy, regained the use of his right hand and was able to resume his career as a two-handed pianist.

Fleisher's dystonia could have been due to a number of causes. Fleischer came to believe that his problem was caused by overpracticing, which he described as "seven or eight hours a day of pumping ivory" (Kozinn, 2020). One possible mechanism associated with this practicing is that using his fingers often and in close conjunction with each other could have changed the locations of their representation in the cortex. This effect of hand dystonia was demonstrated by William Bara-Jimenez and coworkers (1998), who showed that the map of the fingers in area S1 is abnormally organized in some patients with dystonia.

Figure 15.33 shows the results of their experiment, in which they measured the location of the areas in S1 representing the thumb and little finger in a group of six normal participants (**Figure 15.33a**) and six participants with dystonia of the hand (**Figure 15.33b**). The locations for these two fingers, which was determined by stimulating the fingers and measuring the brain activity with scalp electrodes, are separated in the normal participants but are close together in the patients with dystonia.

The beauty of somatosensory maps is that the plastic changes that occur due to stimulation or injury are easy to visualize. But these easy-to-visualize changes are but another example of a principle of brain functioning that we have encountered over and over throughout this book: The brain's structure and functioning are shaped by our experiences and by the nature of our environment. And the outcome of these changes is our ability to understand stimuli we encounter in the environment and to take action within the environment. A few examples that involve plasticity that we have encountered in previous chapters are:

- Chapter 4: Perceiving orientation (p. 74)
- Chapter 5: Sensitivity to regularities in the environment (p. 105)
- Chapter 6: Attentional control by scene schemas (p. 131)
- Chapter 7: Affordances (p. 152)
- Chapter 7: Cognitive maps (p. 157)
- Chapter 7: London taxi drivers' brains (p. 158)
- Chapter 8: Motion response to still pictures (p. 190)
- Chapter 9: Color constancy (p. 215)
- Chapter 10: Sizes of familiar objects (p. 231)
- Chapter 11: Babies recognizing their mother's voice (p. 287)
- Chapter 12: Auditory scene analysis (p. 302)
- Chapter 12: Echolocation in blind people (p. 307)
- Chapter 13: Music rewires the brain (p. 313)
- Chapter 13: Expectancy in music (p. 323)
- Chapter 14: Speech segmentation (p. 345)
- Chapter 14: Statistical properties of speech stimuli (p. 346)

As we continue our discussion of perception in the chapter on the chemical senses, we will yet again encounter perceptions that involve brain plasticity, as we discuss how we smell and how our perception of flavor is influenced by cognition.

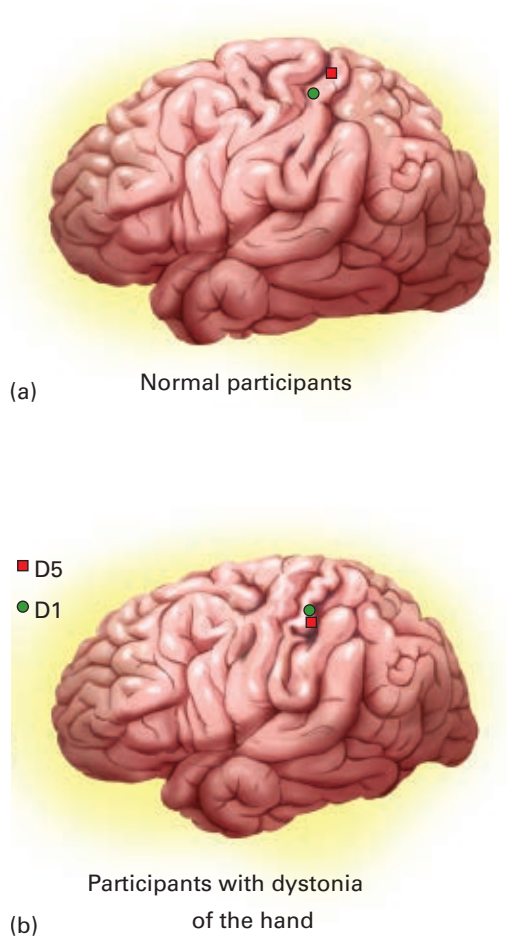

Figure 15.33 Locations of place of representation on the brain of finger D5 (little finger) and D1 (the thumb) of the left hand for (a) control participants and (b) patients with dystonia of the hand. (Adapted from Bar-Jimeniz et al., 1998)

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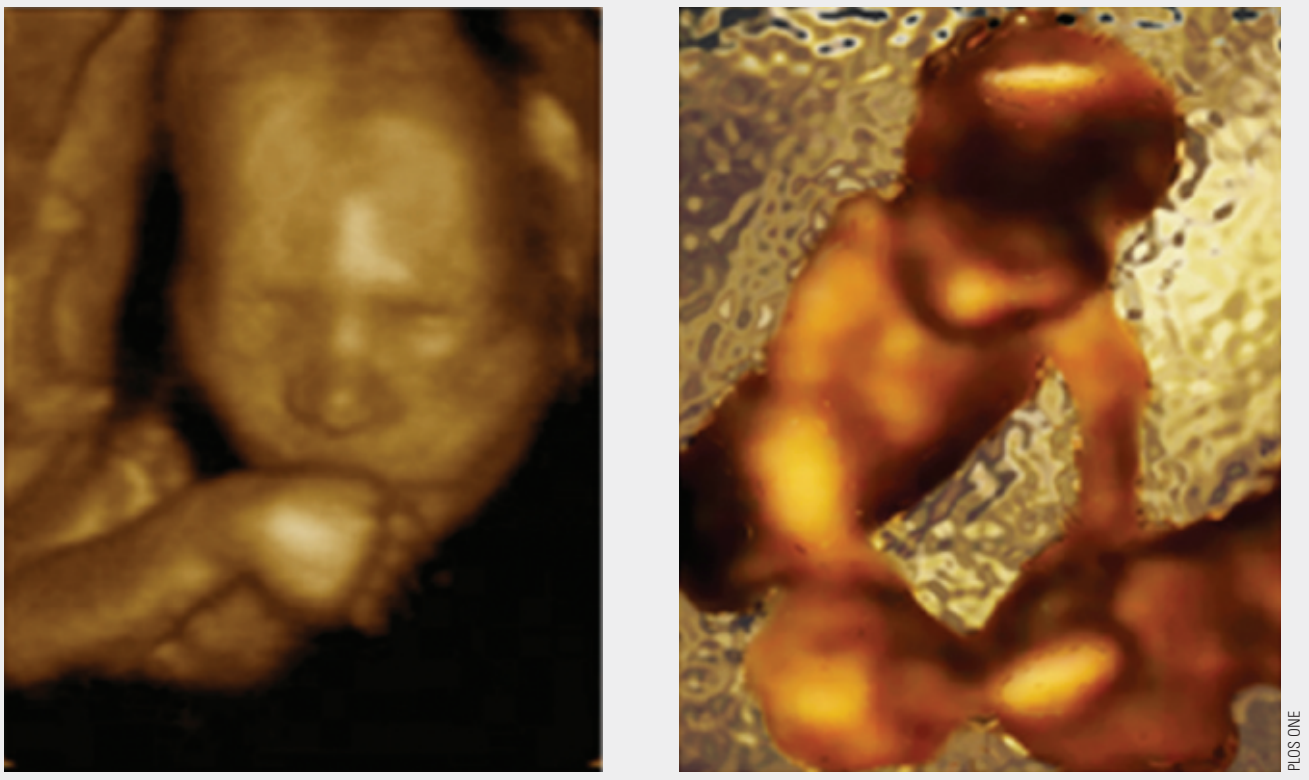
Social touch is important to adults because it not only feels good (p. 372), but it has the important function of being able to reduce pain (p. 379). It could be argued that social touch is also an important part of an infant's experience, and can have far-reaching effects on development that extend into childhood and adulthood.

Touch is the earliest sensory modality to develop, emerging just 8 weeks after gestation, then developing and becoming functional within the womb, and being ready for action at birth (Cascio et al., 2019). Touch and speech are the earliest forms of parent–child interaction, but in contrast to speech, which is a one-way interaction at the beginning, touch is two-way. This is illustrated by the automatic hand closure response to objects (like a parent's finger, for example) placed in the infant's palm (Bremner & Spence, 2017).

What makes the story of infant touch even more interesting is that it begins in the womb. From 26 weeks after gestation, the fetus begins responding to vibration with heart rate acceleration. Later, the fetus begins bringing a hand to the face, and in the last 4 to 5 weeks before birth, begins touching the feet. Viola Marx and Emese Nagy (2017) showed, using ultrasound films, that in the third trimester, the fetus responds when the mother's abdomen is touched.

Even more interesting is what happens with twin fetuses. They are, of course, in close proximity in the womb, so could touch each other accidentally. But ultrasound films have captured a fetus not only moving its hands to its mouth, but also "caressing" the head of its sibling (Castiello et al., 2010) (**Figure 15.34**).

The importance of the infant's ability to touch and sense touch becomes magnified when it is born, because this is when touch becomes social. Sixty-five percent of face-to-face interaction between caregiver and infant involves touch (Cascio et al., 2019). And there is evidence linking touch felt by infants to the social touch experienced by adults that involves CT afferents (p. 371). For example, Merle Fairhurst and coworkers (2014) found that 9-month-old infants respond to movement of a brush along their arm with a decrease in heart rate (indicating a decrease in arousal) if the brush is moved across the arm at 3 cm per second, which is in the range that activates CT afferents. Lower (0.3 cm/sec) or higher (30 cm/sec) rates did not cause this effect.



(a) (b)

Figure 15.34 Frames from ultrasound videos of fetuses in the womb. (a) Fetus that has moved the hand to the mouth. (b) Interaction between twins showing a fetus reaching toward and "caressing" the back of the sibling. (From Castiello et al., 2010)

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Evidence that CT afferents may become involved just after birth is provided by Jetro Tuulari and coworkers (2019), who found that presenting soft brush strokes to the legs of 11- to 16-day-old infants activates the posterior insula (Figure 15.26), which is associated with social touch in adults.

And just as social touch can reduce pain in adults, the skin-to-skin contact that occurs when newborn infants are held close by the mother (sometimes called kangaroo care) has been shown to cause an 82 percent decrease in crying in response to a medical heel lance procedure (Gray et al., 2000; also see Ludington-Hoe & Husseini, 2005).

The most important outcome of an infant's experience of social touch is how it shapes social, communicative, and cognitive development in the months and years that follow (Cascio et al., 2019). A dramatic demonstration of this effect of social touch is provided by premature infants who are deprived of early social touch when they are separated from their mothers and placed in incubators. When these premature infants are massaged, they have more weight gain, better cognitive development, better motor skills, and better sleep than premature infants who are not massaged (Field, 1995; Wang et al., 2013).

At the beginning of this Developmental Dimension we noted that touch and speech are the earliest forms of parent–child interaction. We saw in Chapter 14 that infant-directed speech (IDS) has many beneficial effects on the developing infant (p. 353). We've seen here that social touch has its own positive effects. Clearly, using infant-directed speech in conjunction with social touch is a powerful combination for enhancing the course of an infant's development.

TEST YOURSELF 15.3

1. What does it mean to say that pain is multimodal? Describe the hypnosis experiments that identified areas involved in the sensory component of pain and the emotional component of pain.
2. Describe the role of chemicals in the perception of pain. Be sure you understand how endorphins and naloxone interact at receptor sites, and a possible mechanism that explains why pain is reduced by placebos.
3. Describe the experiment which demonstrated that a placebo effect can operate on local parts of the body.
4. Describe the experiment which shows that social touch can cause a decrease in pain.
5. Describe the experiments which showed how observing someone being touched or observing someone experiencing pain can affect activity in the observer's brain. What do these results tell us about empathy?
6. What is the evidence supporting the idea that social and physical pain share some mechanisms? What evidence questions this idea?
7. How has the plasticity of the somatosensory cortex been demonstrated in monkeys? In humans? What is hand dystonia, and how is it related to brain plasticity?
8. What are some examples of brain plasticity in vision and hearing that were described in previous chapters?
9. When does touch develop in infants, and what is the evidence that social touch has an impact on later development?

THINK ABOUT IT

1. One of the themes in this book is that it is possible to use the results of psychophysical experiments to suggest the operation of physiological mechanisms or to link physiological mechanisms to perception. Cite an example of how psychophysics has been used in this way for each of the senses we have considered so far—vision, hearing, and the cutaneous senses.
2. Some people report situations in which they were injured but didn't feel any pain until they became aware of their injury. How would you explain this kind of situation in terms of top-down and bottom-up processing? How could you relate this situation to the studies we have discussed? (p. 374)
3. Even though the senses of vision and cutaneous perception are different in many ways, there are a number of parallels between them. Cite examples of parallels between vision and cutaneous sensations (touch and pain) for the following: "tuned" receptors, mechanisms of detail perception, receptive fields, and top-down processing. Also, can you think of situations in which vision and touch interact with one another?

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KEY TERMS

Active touch (p. 368)
Affective (or emotional) component of pain (p. 377)
Affective function of touch (p. 372)
CT afferents (p. 371)
Cutaneous receptive field (p. 358)
Cutaneous senses (p. 358)
Dermis (p. 358)
Direct pathway model of pain (p. 373)
Discriminative function of touch (p. 372)
Duplex theory of texture perception (p. 366)
Empathy (p. 379)
Endorphin (p. 377)
Epidermis (p. 358)
Exploratory procedures (EPs) (p. 369)
Gate control model (p. 374)
Grating acuity (p. 363)
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Haptic perception (p. 368)
Homunculus (p. 362)
Inflammatory pain (p. 373)
Interpersonal touching (p. 371)
Kinesthesis (p. 358)
Knowledge-based processing (p. 372)
Mechanoreceptor (p. 358)
Medial lemniscal pathway (p. 359)
Meissner corpuscle (RA1) (p. 358)
Merkel receptor (SA1) (p. 358)
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Phantom limb (p. 373)
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Placebo effect (p. 375)
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Rapidly adapting (RA1) fiber (p. 359)
Ruffini cylinder (SA2) (p. 359)
SA1 fiber (p. 358)
SA2 fiber (p. 359)
Secondary somatosensory cortex (S2) (p. 361)
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Tactile acuity (p. 363)
Temporal cue (p. 366)
Top-down processing (p. 372)
Transmission cell (p. 374)
Two-point threshold (p. 363)
Ventrolateral nucleus (p. 359)

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These people are enjoying not only the social experience of eating with others, but also the sensory experiences created by taste and smell. Taste is created by receptors on the tongue, smell by receptors in the nose, and taste and smell work together to create flavor, which is the dominant perception we experience when eating or drinking.

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Learning Objectives

After studying this chapter, you will be able to ...

- Describe the structure of the taste system and how activity in this system is related to taste quality.
- Describe genetic research on individual differences in taste.
- Describe the following aspects of basic olfactory abilities: detecting odors, identifying odors, individual differences in olfaction, and how olfaction is affected by COVID-19 and Alzheimer's disease.
- Describe how olfactory quality is analyzed by the mucosa and olfactory bulb.
- Understand how odors are represented in the cortex.
- Understand the connection between olfaction and memory.
- Describe what flavor is and how it is related to taste, olfaction, cognition, and satiation.
- Describe multimodal interactions between the senses.
- Describe how researchers have measured infant chemical sensitivity.

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CHAPTER 16

The Chemical Senses

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TEST YOURSELF 16.1

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16.9 The Perception of Flavor

DEMONSTRATION: Tasting With and Without the Nose

Taste and Olfaction Meet in the Mouth and Nose

Taste and Olfaction Meet in the Nervous System

Flavor Is Influenced by Cognitive Factors

Flavor Is Influenced by Food Intake: Sensory-Specific Satiety

SOMETHING TO CONSIDER: Community of the Senses

Correspondences

Influences

DEVELOPMENTAL DIMENSION: Infant Chemical Sensitivity

TEST YOURSELF 16.3

THINK ABOUT IT

Some Questions We Will Consider:

- Are there differences in the way different people experience the taste of food? (p. 396)
- How is the sense of smell affected by other senses like vision and hearing? (p. 412)
- How does what a pregnant woman eats affect the taste preferences of her baby? (p. 414)

Katherine Hansen always had such an acute sense of smell that she could recreate any restaurant dish at home without the recipe, just by recalling the scents and flavors (Rabin, 2021). But in March of 2020, her sense of smell vanished, a condition called **anosmia**, followed by her sense of taste, followed by the onset of coronavirus (COVID-19). Over half of people who get COVID experience partial or total loss of smell (olfaction) and taste (Parma et al., 2020; Pinna et al., 2020), caused by mechanisms we will discuss later in the chapter (see page 399). Most COVID patients regain their senses of smell and taste within a short time, but a few, like Katherine, remain without these senses for long periods. In Katherine's case, her senses of smell and taste were still absent 10 months after they had vanished.

Although smell and taste are often thought of as "minor" senses, the effect of losing smell and taste argues otherwise, as this loss is associated with dramatic effects on a person's quality of life (Croy et al., 2013). In a study of the experiences of 9,000 COVID patients who had lost their senses of smell and taste, many said that they not only lost the pleasure of eating, but also the pleasure of socializing, and reported feeling isolated and detached from reality. One person put it this way:

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"I feel alien from myself. It's also a kind of loneliness in the world, like a part of me is missing, as I can no longer smell and experience the emotions of everyday basic living" (Rabin, 2021).

People who have lost smell and taste, both from COVID and other causes, not only become unmotivated to eat, which can lead to health problems (Beauchamp & Mennella, 2011), but also become more prone to hazardous events, such as food poisoning or failure to detect fire or leaking natural gas. In one study, 45 percent of people with anosmia had experienced at least one such hazardous event, compared to 19 percent of people with normal olfactory function (Cameron, 2018; Santos et al., 2004).

Molly Birnbaum (2011), who lost her sense of smell after being hit by a car while crossing the street, also noted the loss of everyday smells she had taken for granted. She described New York City without smell as "a blank slate without the aroma of car exhaust, hot dogs or coffee" and when she gradually began to regain some ability to smell she reveled in every new odor. "Cucumber!" she writes, "Their once common negligible scent had returned—intoxicating, almost ambrosial. The scent of melon could bring me to tears" (Birnbaum, 2011, p. 110). These descriptions help us see that olfaction is more important in our lives than most of us realize. Although it may not be essential to our survival, life is often enhanced by our ability to smell and becomes a little more dangerous if we lose the olfactory warning system that can alert us to danger.

16.1 Some Properties of the Chemical Senses

The chemical senses involve three components: **taste**, which occurs when molecules—often associated with food—enter the mouth in solid or liquid form and stimulate receptors on the tongue (**Figure 16.1**); **olfaction**, which occurs when airborne molecules enter the nose and stimulate receptor neurons in the olfactory mucosa, located on the roof of the nasal cavity; and **flavor**, which is the impression we experience from the combination of taste and olfaction.

One property that distinguishes the chemical senses from vision, hearing, and the cutaneous senses occurs right at the beginning of the systems, when the receptors are being stimulated. For vision, light stimulates rod and cone receptors inside the eyeball. For hearing, pressure changes are transmitted to hair cells located deep inside the cochlea. For the cutaneous senses, stimuli applied to the skin are transmitted to receptors or nerve endings hidden under the skin. But for taste and smell, molecules stimulate receptors that are exposed to the environment.

Because the receptors that serve taste and smell are constantly exposed not only to the chemicals they are designed to sense but also to harmful materials such as bacteria and dirt, they undergo a cycle of birth, development, and death over 5–7 weeks for olfactory receptors and 1–2 weeks for taste receptors. This constant renewal of the receptors, called **neurogenesis**, is unique to these senses.

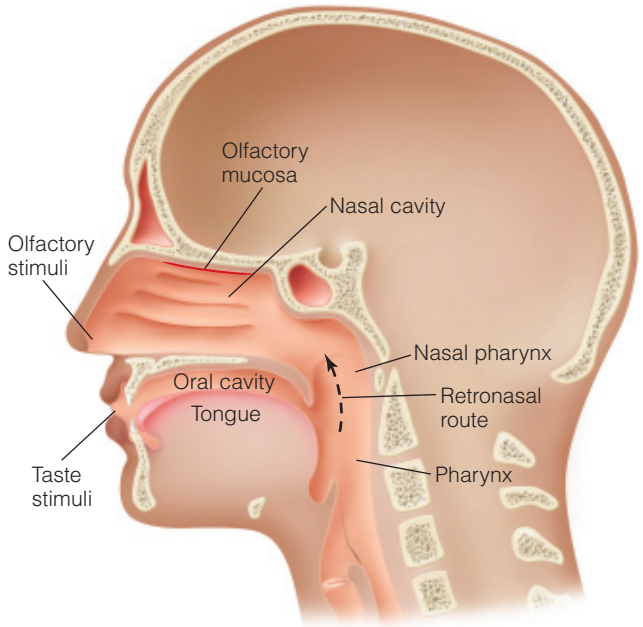

Figure 16.1 Odorant molecules released by food in the oral cavity and pharynx can travel through the nasal pharynx (dashed arrow) to the olfactory mucosa in the nasal cavity. This is the retronasal route to the olfactory receptors, which will be discussed later in the chapter.

Because the stimuli responsible for tasting and smelling are taken into the body, these senses are often seen as "gatekeepers" that (1) identify things that the body needs for survival and that should therefore be consumed and (2) detect things that would be bad for the body and that should therefore be rejected. The gatekeeper function of taste and smell is aided by a large affective, or emotional, component—things that are bad for us often taste or smell unpleasant, and things that are good for us generally taste or smell good. In addition to creating "good" and "bad" affect, smelling an odor associated with a past place or event can trigger memories, which in turn may create emotional reactions.

In this chapter, we will first consider taste and then olfaction. We will describe the psychophysics and anatomy of each system and then how different taste and smell qualities are coded in the nervous system. Finally, we consider flavor, which results from the interaction of taste and olfaction.

16.2 Taste Quality

Everyone is familiar with taste. We experience it every time we eat. (Although later in the chapter we will see that what we usually experience when we eat is actually "flavor," which is a combination of taste and olfaction.) Taste occurs when molecules enter the mouth in solid or liquid form and stimulate taste receptors on the tongue. The perceptions resulting from this stimulation have been described in terms of five basic taste qualities.

Most taste researchers describe taste quality in terms of five basic taste sensations: salty, sour, sweet, bitter, and umami (which has been described as meaty, brothy, or savory, and is

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often associated with the flavor-enhancing properties of MSG, monosodium glutamate).

Basic Taste Qualities

In an early experiment on taste quality, before umami became the fifth basic taste, Donald McBurney (1969) presented taste solutions to participants and asked them to make magnitude estimates of the intensity of each of the four taste qualities for each solution (see page 16 and Appendix B for descriptions of the magnitude estimation procedure). He found that some substances have a predominant taste quality and that other substances result in combinations of the four taste qualities. For example, sodium chloride (salty), hydrochloric acid (sour), sucrose (sweet), and quinine (bitter) are compounds that come the closest to having only one of the four basic tastes. However, the compound potassium chloride (KCl) has substantial salty and bitter components, whereas sodium nitrate ($NaNO_3$) results in a taste consisting of a combination of salty, sour, and bitter (**Figure 16.2**).

Results such as these have led most researchers to accept the idea of basic tastes. As you will see when we discuss the neural code for taste quality, most of the research on this problem takes the idea of basic tastes as the starting point. (Although Erickson, 2000, presents some arguments against the idea of basic tastes.)

Connections Between Taste Quality and a Substance's Effect

We noted that taste and olfaction can be thought of as "gatekeepers." This is especially true for taste because we often use taste to choose which foods to eat and which to avoid (Breslin, 2001). Taste accomplishes its gatekeeper function by the connection between taste quality and a substance's effect.

Sweetness is often associated with compounds that have nutritive or caloric value and that are, therefore, important for sustaining life. Sweet compounds cause an automatic acceptance response and also trigger anticipatory metabolic responses that prepare the gastrointestinal system for processing these substances.

Bitter compounds have the opposite effect—they trigger automatic rejection responses to help the organism avoid harmful substances. Examples of harmful substances that taste bitter are the poisons strychnine, arsenic, and cyanide.

Salty tastes often indicate the presence of sodium. When people are deprived of sodium or lose a great deal of sodium through sweating, they often seek out foods that taste salty in order to replenish the salt their body needs.

Although there are many examples of connections between a substance's taste and its function in the body, this connection is not perfect. People have often made the mistake of eating good-tasting poisonous mushrooms, and there are artificial sweeteners, such as saccharine and sucralose, that have no metabolic value. There are also bitter foods that are not dangerous and do have metabolic value. People can also learn to modify their responses to certain tastes, as when they develop a taste for foods they may have initially found unappealing, such as the bitter tastes in beer and coffee.

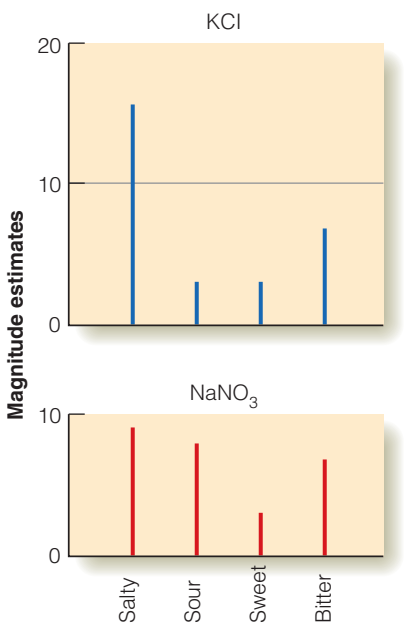

Figure 16.2 The contribution of each of the four basic tastes to the tastes of KCl and $NaNO_3$, determined by the method of magnitude estimation. The height of the line indicates the size of the magnitude estimate for each basic taste. (From McBurney, 1969)

16.3 The Neural Code for Taste Quality

One of the central concerns in taste research has been identifying the physiological code for taste quality. We will first describe the structure of the taste system and then will describe two proposals regarding how taste quality is coded in this system.

Structure of the Taste System

The process of tasting begins with the tongue (**Figure 16.3a** and **Table 16.1**). The surface of the tongue contains many ridges and valleys caused by the presence of structures called papillae, which fall into four categories: (1) filiform papillae, which are shaped like cones and are found over the entire surface of the tongue, giving it its rough appearance; (2) fungiform papillae, which are shaped like mushrooms and are found at the tip and sides of the tongue (see **Figure 16.4**); (3) foliate papillae, which are a series of folds along the back of the tongue on the sides; and (4) circumvallate papillae, which are shaped like flat mounds surrounded by a trench and are found at the back of the tongue.

All of the papillae except the filiform papillae contain taste buds (**Figures 16.3b** and **16.3c**), and the whole tongue contains about 10,000 taste buds (Bartoshuk, 1971). Because

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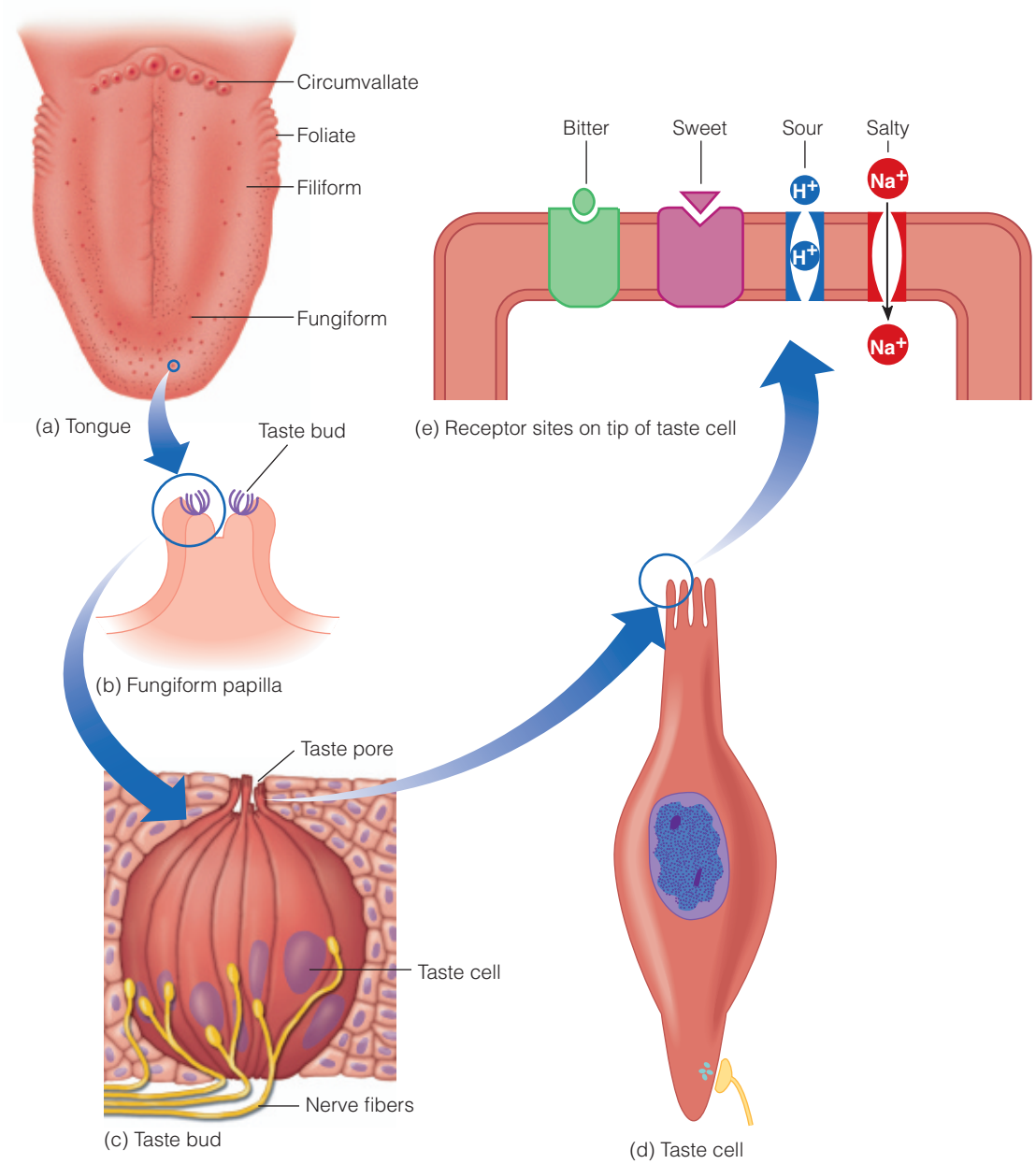

Figure 16.3 (a) The tongue, showing the four different types of papillae. (b) A fungiform papilla on the tongue; each papilla contains a number of taste buds. (c) Cross section of a taste bud showing the taste pore where the taste stimulus enters. (d) The taste cell; the tip of the taste cell is positioned just under the pore. (e) Close-up of the membrane at the tip of the taste cell, showing the receptor sites for bitter, sweet, sour, and salty substances. Stimulation of these receptor sites, as described in the text, triggers a number of different reactions within the cell (not shown) that lead to movement of charged molecules across the membrane, which creates an electrical signal in the receptor.

the filiform papillae contain no taste buds, stimulation of the central part of the tongue, which contains only these papillae, causes no taste sensations. However, stimulation of the back or perimeter of the tongue results in a broad range of taste sensations.

Each taste bud contains 50 to 100 **taste cells**, which have tips that protrude into the **taste pore** (Figure 16.3c). Transduction occurs when chemicals contact receptor sites located on the tips of these taste cells (**Figure 16.3d** and **16.3e**). Electrical signals generated in the taste cells are transmitted from the tongue toward the brain in a number of different nerves: (1) the chorda tympani nerve (from taste cells on the front and sides of the tongue); (2) the glossopharyngeal nerve (from the back of the tongue); (3) the vagus nerve (from the mouth and throat); and (4) the superficial petrosal nerve (from the soft palette—the top of the mouth).

The fibers from the tongue, mouth, and throat make connections in the brain stem in the **nucleus of the solitary tract**

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Table 16.1 Structures in the Taste System

STRUCTURE	DESCRIPTION
Tongue	The receptor sheet for taste. Contains papillae and all of the other structures described below.
Papillae	The structures that give the tongue its rough appearance. There are four kinds, each with a different shape.
Taste buds	Contained on the papillae. There are about 10,000 taste buds.
Taste cells	Cells that make up a taste bud. There are a number of cells for each bud, and the tip of each one sticks out into a taste pore. One or more nerve fibers are associated with each cell.
Receptor sites	Sites located on the tips of the taste cells. There are different types of sites for different chemicals. Chemicals contacting the sites cause transduction by affecting ion flow across the membrane of the taste cell.

Figure 16.4 The surface of the tongue. The red dots are fungiform papillae. (From Shahbake, 2008)

(**Figure 16.5**). From there, signals travel to the thalamus and then to two areas in the frontal lobe that are considered to be the primary taste cortex—the **insula** and the **frontal operculum**—which are partially hidden behind the temporal lobe (Finger, 1987; Frank & Rabin, 1989).

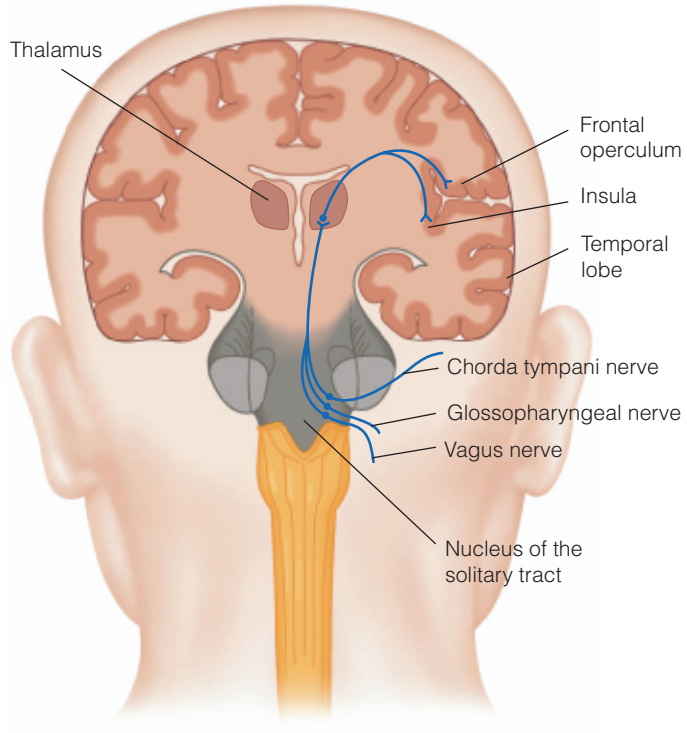

Figure 16.5 The central pathway for taste signals, showing the nucleus of the solitary tract, where nerve fibers from the tongue and the mouth synapse in the medulla at the base of the brain. From the nucleus of the solitary tract, these fibers synapse in the thalamus and then the insula and frontal operculum, which are the cortical areas for taste. (From Frank & Rabin, 1989)

Population Coding

In Chapter 2 we distinguished between two types of coding: *specificity coding*, the idea that quality is signaled by the activity in individual neurons that are tuned to respond to specific qualities; and *population coding*, the idea that quality is signaled by the pattern of activity distributed across many neurons. In that discussion, and in others throughout the book, we have generally favored population coding. The situation for taste, however, is not clear-cut, and there are arguments in favor of both types of coding (Frank et al., 2008).

Let's consider some evidence for population coding. Robert Erickson (1963) conducted one of the first experiments that demonstrated this type of coding by presenting a number of different taste stimuli to a rat's tongue and recording the response of the chorda tympani nerve. **Figure 16.6** shows how 13 nerve fibers responded to ammonium chloride (NH_4Cl), potassium chloride (KCl), and sodium chloride (NaCl). Erickson called these patterns the **across-fiber patterns**, which is another name for population coding. The red and green lines show that the across-fiber patterns for ammonium chloride and potassium chloride are similar to each other but different from the pattern for sodium chloride, indicated by the open circles.

Erickson reasoned that if the rat's perception of taste quality depends on the across-fiber pattern, then two substances with similar patterns should taste similar. Thus, the electrophysiological results would predict that ammonium chloride and potassium chloride should taste similar and that both should taste different from sodium chloride. To test this

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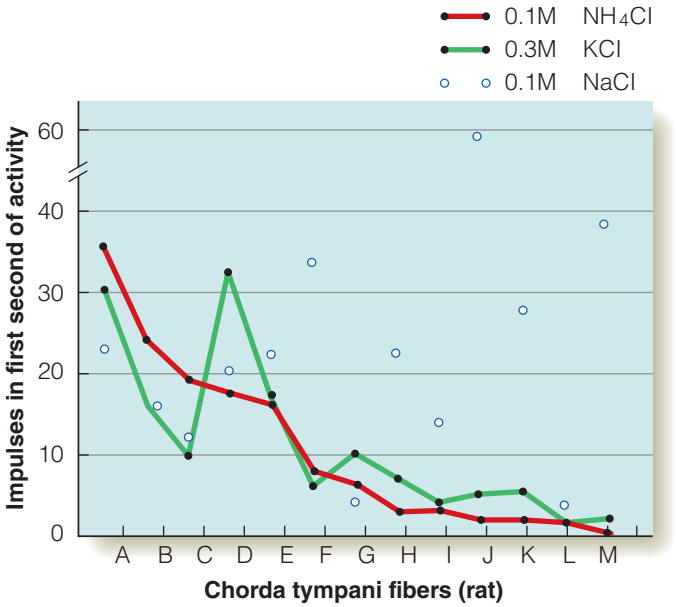

Figure 16.6 Across-fiber patterns of the response of fibers in the rat's chorda tympani nerve to three salts. Each letter on the horizontal axis indicates a different single fiber. (Based on Erickson, 1963)

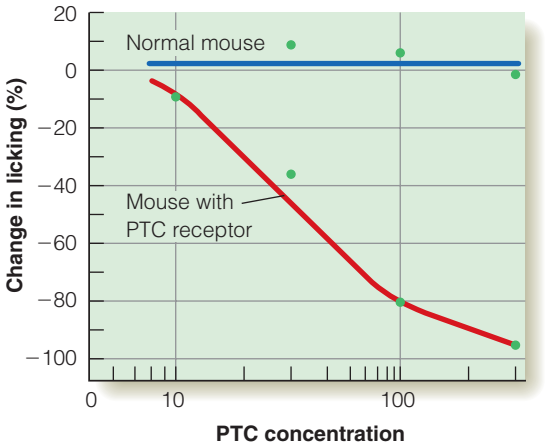

Figure 16.7 Mouse behavioral response to PTC. The blue curve indicates that a normal mouse will consume PTC even in high concentrations. The red curve indicates that a mouse that has a human bitter-PTC receptor avoids PTC, especially at high concentrations. (Adapted from Mueller et al., 2005)

hypothesis, Erickson shocked rats while they were drinking potassium chloride and then gave them a choice between ammonium chloride and sodium chloride. If potassium chloride and ammonium chloride taste similar, the rats should avoid the ammonium chloride when given a choice. This is exactly what they did. And when the rats were shocked for drinking ammonium chloride, they subsequently avoided the potassium chloride, as predicted by the electrophysiological results.

But what about the perception of taste in humans? When Susan Schiffman and Robert Erickson (1971) asked humans to make similarity judgments between a number of different solutions, they found that substances that were perceived to be similar were related to patterns of firing for these same substances in the rat. Solutions judged more similar psychophysically had similar patterns of firing, as population coding would predict.

Specificity Coding

Most of the evidence for specificity coding comes from research that has recorded neural activity early in the taste system. We begin at the receptors by describing experiments that have revealed receptors for sweet, bitter, and umami.

The evidence supporting the existence of receptors that respond specifically to a particular taste has been obtained by using genetic cloning, which makes it possible to add or eliminate specific receptors in mice. Ken Mueller and coworkers (2005) did a series of experiments using a chemical compound called PTC that tastes bitter to humans but is not bitter to mice. The lack of bitter PTC taste in mice is inferred from the fact that mice do not avoid even high concentrations of PTC in behavioral tests (blue curve in **Figure 16.7**). Because a specific receptor in the family of bitter receptors had been identified as being responsible for the bitter taste of PTC in humans, Mueller decided to see what would happen if he used genetic cloning techniques to create a strain of mice that had this human bitter-PTC receptor. When he did this, the mice with this receptor avoided high concentrations of PTC (red curve in Figure 16.7; see **Table 16.2a**).

In another experiment, Mueller created a strain of mice that lacked a bitter receptor that responds to a compound called cyclohexamide (Cyx). Mice normally have this receptor, so they avoid Cyx. But the mice lacking this receptor did not avoid Cyx (**Table 16.2b**). In addition, Cyx no longer caused any firing in nerves receiving signals from the tongue. Therefore, when the taste receptor for a substance is eliminated, this is reflected in both nerve firing and the animal's behavior.

It is important to note that in all these experiments, adding or eliminating bitter receptors had no effect on neural firing or behavior to sweet, sour, salty, or umami stimuli. Other research using similar techniques has identified receptors for sugar and umami (Zhao et al., 2003).

The results of these experiments in which adding a receptor makes an animal sensitive to a specific quality and eliminating a receptor makes an animal insensitive to a specific quality have been cited as support for specificity coding—that there

Table 16.2 Results of Mueller's Experiments

CHEMICAL	NORMAL MOUSE	CLONED MOUSE
(a) PTC	No PTC receptor	Has PTC receptor
	Doesn't avoid PTC	Avoids PTC
(b) Cyx	Has Cyx receptor	No Cyx receptor
	Avoids Cyx	Doesn't avoid Cyx

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are receptors that are specifically tuned to sweet, bitter, and umami tastes. However, not all researchers agree that the picture is so clear-cut. For example, Eugene Delay and coworkers (2006) showed that with different behavioral tests, mice that appeared to have been made insensitive to sugar by eliminating a "sweet" receptor can actually still show a preference for sugar. Based on this result, Delay suggests that perhaps there are a number of different receptors that respond to specific substances like sugar.

Another line of evidence for specificity coding in taste has come from research on how single neurons respond to taste stimuli. Recordings from neurons at the beginning of the taste systems of animals, ranging from rats to monkeys, have revealed neurons that are specialized to respond to specific stimuli, as well as neurons that respond to a number of different types of stimuli (Lundy & Contreras, 1999; Sato et al., 1994; Spector & Travers, 2005).

Figure 16.8 shows how three neurons in the rat taste system respond to sucrose (sweet to humans), sodium chloride (NaCl; salty), hydrochloric acid (HCl; sour in low concentrations), and quinine (QHCl; bitter) (Lundy & Conteras, 1999). The neuron in **Figure 16.8a** responds selectively to sucrose, the one in **Figure 16.8b** responds selectively to NaCl, and the neuron in **Figure 16.8c** responds to NaCl, HCl, and QHCl. Neurons like the ones in Figures 16.8a and 16.8b, which respond selectively to stimuli associated with sweetness (sucrose) and saltiness (NaCl), provide evidence for specificity coding. Neurons have also been found that respond selectively to sour (HCl) and bitter (QHCl) (Spector & Travers, 2005).

Another finding in line with specificity theory is the effect of presenting a substance called amiloride, which blocks the flow of sodium into taste receptors. Applying amiloride to the tongue causes a decrease in the responding of neurons in the rat's brainstem (nucleus of the solitary tract) that respond best to salt (**Figure 16.9a**) but has little effect on neurons that respond best to a combination of salty and bitter tastes (**Figure 16.9b**; Scott & Giza, 1990). Thus, eliminating the flow of sodium across the membrane selectively eliminates responding of salt-best neurons but does not affect the response of neurons that respond best to other tastes. As it turns out, the sodium channel that is blocked by amiloride is important for determining saltiness in rats and other animals, but not in humans. More recent research has identified another channel that serves the salty taste in humans (Lyall et al., 2004, 2005).

What does all of this mean? The results of the experiments involving cloning, recording from single neurons, and the effect of amiloride seem to be shifting the balance in the population versus specificity argument toward specificity (Chandrashekar et al., 2006). However, the issue is still not settled. For example, David Smith and Thomas Scott (2003) argue for population coding based on the finding that at more central locations in the taste system, neurons are tuned broadly, with many neurons responding to more than one taste quality. Smith and coworkers (2000) point out that just because there are neurons that respond best to one compound like salty or sour, this doesn't mean that these tastes are signaled by just

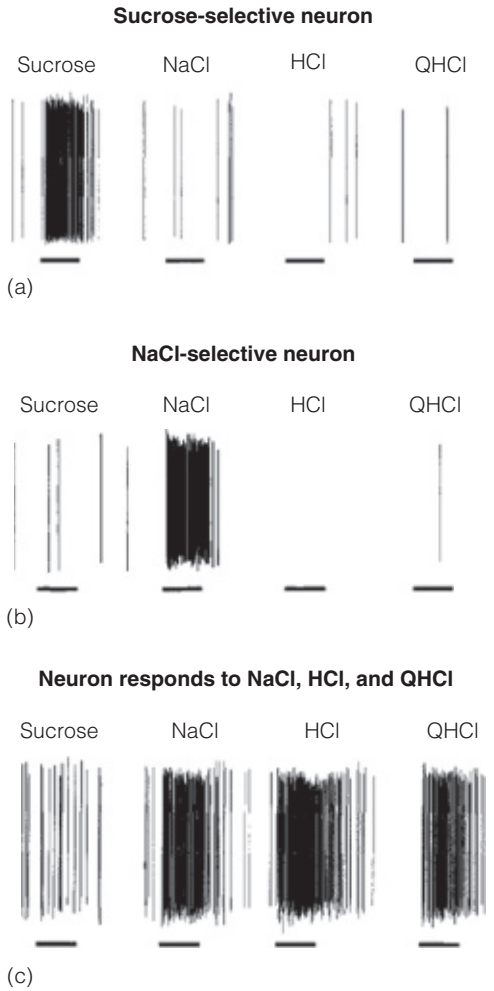

Figure 16.8 Responses of three neurons recorded from the cell bodies of chorda tympani nerve fibers in the rat. Solutions of sucrose, salt (NaCl), hydrochloric acid (HCl), and quinine hydrochloride (QHCl) were flowed over the rat's tongue for 15 seconds, as indicated by the horizontal lines below the firing records. Vertical lines are individual nerve impulses. (a) Neuron responds selectively to sweet stimulus; (b) neuron responds selectively to salt; (c) neuron responds to salty, sour, and bitter stimuli. (From Lundy & Contreras, 1999)

one type of neuron. They illustrate this by drawing an analogy between taste perception and the mechanism for color vision. Even though presenting a long-wavelength light that appears red may cause the highest activation in the long-wavelength cone pigment (see Figure 9.15 page 206), our perception of red still depends on the combined response of both the long- and medium-wavelength pigments. Similarly, salt stimuli may cause high firing in neurons that respond best to salt, but other neurons are probably also involved in creating saltiness.

Because of arguments such as this, some researchers believe that even though there is good evidence for specific taste receptors, population coding is involved in determining taste as well, especially at higher levels of the system. One suggestion is that basic taste qualities might be determined by a specific code, but population coding could determine subtle differences

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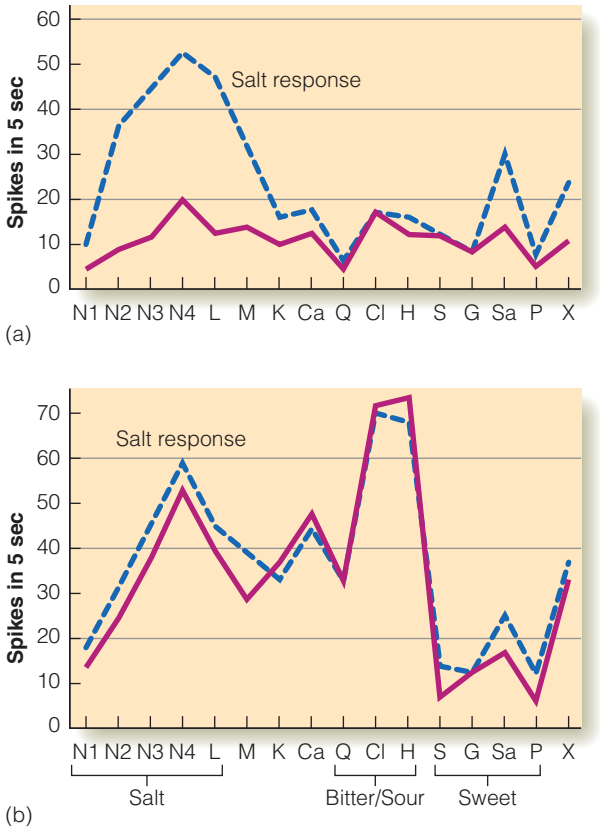

Figure 16.9 The blue dashed lines show how two neurons in the rat's nucleus of the solitary tract respond to a number of different taste stimuli (along the horizontal axis). The neuron in (a) responds strongly to compounds associated with salty tastes. The neuron in (b) responds to a wide range of compounds. The solid red lines show how these two neurons fire after the sodium-blocker amiloride is applied to the tongue. This compound inhibits the responses of the neuron that responds to salt (a) but has little effect on neuron (b). (Adapted from Scott & Giza, 1990)

between tastes within a category (Pfaffmann, 1974; Scott & Plata-Salaman, 1991). This would help explain why not all substances in a particular category have the same taste. For example, the taste of all sweet substances is not identical (Lawless, 2001).

16.4 Individual Differences in Taste

The "taste worlds" of humans and animals are not necessarily the same. For example, domestic cats, unlike most mammals, don't prefer the sweetness of sugar, even though they display human-like taste behavior to other compounds, such as avoiding compounds that taste bitter or very sour to humans. Genetic research has shown that this "sweet blindness" occurs because cats lack a functional gene for formation of a sweet receptor and so, lacking a sweet receptor, have no mechanism for detecting sweetness (Li et al., 2005).

This interesting fact about cats has something to tell us about human taste perception, because it turns out that there are genetic differences that affect people's ability to sense the taste of certain substances. One of the best-documented effects involves people's ability to taste the bitter substance phenylthiocarbamide (PTC), which we discussed earlier in connection with Mueller's experiments on specificity coding (see page 394). The discovery of the PTC effect has been described as follows:

> The different reactions to PTC were discovered accidentally in 1932 by Arthur L. Fox, a chemist working at the E. I. DuPont deNemours Company in Wilmington, Delaware. Fox had prepared some PTC, and when he poured the compound into a bottle, some of the dust escaped into the air. One of his colleagues complained about the bitter taste of the dust, but Fox, much closer to the material, noticed nothing. Albert F. Blakeslee, an eminent geneticist of the era, was quick to pursue this observation. At a meeting of the American Association for the Advancement of Science (AAAS) in 1934, Blakeslee prepared an exhibit that dispensed PTC crystals to 2,500 of the conferees. The results: 28 percent of them described it as tasteless, 66 percent as bitter, and 6 percent as having some other taste. (Bartoshuk, 1980, p. 55)

People who can taste PTC are described as *tasters*, and those who cannot are called *nontasters*. Additional experiments have also been done with a substance called 6-*n*-propylthiouracil, or PROP, which has properties similar to those of PTC (Lawless, 1980, 2001). Researchers have found that about one-third of Americans report that PROP is tasteless and two-thirds can taste it. What causes these differences in people's ability to taste PROP? One explanation for these differences is that people who can taste PROP have higher densities of taste buds than those who can't taste it (Bartoshuk & Beauchamp, 1994) (**Figure 16.10**).

A factor that determines individual differences in taste, in addition to receptor density, is the presence of specialized receptors. Advances in genetic techniques have made it possible to determine the locations and identities of genes on human chromosomes that are associated with taste and smell receptors. These studies have shown that PROP and PTC tasters have specialized receptors that are absent in nontasters (Bufe et al., 2005; Kim et al., 2003).

What does this mean for everyday taste experience? If PROP tasters also perceived other compounds as being more bitter than nontasters, then certain foods might taste more bitter to the tasters. The evidence on this question, however, has been mixed. Some studies have reported differences between how tasters and nontasters rate the bitterness of other compounds (Bartoshuk, 1979; Hall et al., 1975), and others have not observed this difference (Delwiche et al., 2001b). However, it does appear that people who are especially sensitive to PROP, called *supertasters*, may actually be more sensitive to most bitter substances, as if the amplification in the bitter

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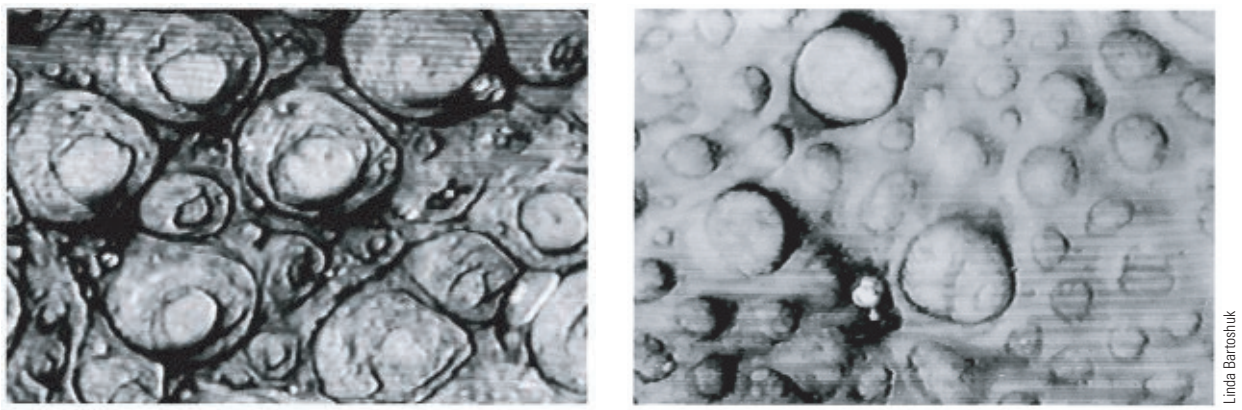

(a) (b)

Linda Bartoshuk

Figure 16.10 (a) Video micrograph of the tongue showing the fungiform papillae of a "supertaster"—a person who is very sensitive to the taste of PROP. (b) Papillae of a "nontaster"—someone who cannot taste PROP. The supertaster has both more papillae and more taste buds than the nontaster. (Courtesy of Linda Bartoshuk)

taste system is turned up for all bitter compounds (Delwiche et al., 2001a).

But the research on PROP nontasters and supertasters has turned out to be just the tip of the iceberg with regard to individual differences. For example, genetic differences between individuals have also been linked to differences in the perception of the sweetness of sucrose (Fushan et al., 2009).

Thus, the next time you disagree with someone about the taste of a particular food, don't automatically assume that your disagreement is simply a reflection of your individual preferences. It may reflect not a difference in *preference* (you *like* sweet things more than John does) but a difference in *perception* (you *perceive* sweet tastes as more intense than John does), which could be caused by differences in the types and numbers of taste receptors on the tongue or other differences in your taste systems.

TEST YOURSELF 16.1

1. What is anosmia? How does anosmia change people's life experience?
2. What are some ways that the chemical senses differ from vision, touch, and the cutaneous senses?
3. What is neurogenesis, and what function does it serve?
4. What are the five basic taste qualities?
5. How is taste quality linked to a substance's physiological effect?
6. Describe the anatomy of the taste system, including the receptors and central destinations.
7. What is the evidence for population coding and specificity coding in taste? Is it possible to choose between the two?
8. What kinds of evidence support the idea that different people may have different taste experiences? What mechanisms may be responsible for these differences?

16.5 The Importance of Olfaction

At the beginning of the chapter we noted that taste and olfaction have often been described as being less important than vision and hearing. The importance of olfaction has also been minimized in many textbooks, which describe human olfaction as being **microsmatic** (having a poor sense of smell that is not crucial to survival), while describing olfaction in other animals, and especially dogs, as **macrosmatic**—having a well-developed sense of smell (McGann, 2017).

But recent measurements of the sensitivity of humans and animals to different odors indicates that humans are more sensitive to many odors than a wide range of animals, including mice, monkeys, rabbits, and seals. And although dogs are far more sensitive than humans to some odors, human's sensitivity equals dog's for others (Laska, 2017).

Caroline Bushdid and coworkers (2014) tested participants to determine how many components of a substance they could change before they could detect the difference between two substances. Based on their results, plus an estimate of the number of possible odors, they proposed that humans can discriminate the difference in the smells of more than 1 trillion olfactory stimuli. Other researchers have questioned this number, saying it is too high (Gerkin & Castro, 2015; Meister, 2015). But even if this is an overestimate, human olfaction is extremely impressive, especially when compared to vision (we can discriminate several million different colors) and hearing (we can discriminate almost half a million different tones), and to make the case for human olfaction more even convincing, it has been shown that humans, like dogs, can track scents in a field (Porter et al., 2007).

This recent evidence has led one olfaction researcher to state that "...contrary to traditional textbook wisdom, humans are not generally inferior in their olfactory sensitivity

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compared to animals" (Laska, 2017), and another one to state that "our sense of smell is much more important than we think" (McGann, 2017). In the next section we will look further at some of our olfactory abilities.

16.6 Olfactory Abilities

How well can we smell? We've already noted that human sensitivity to odors can rival that of many animals. We will now look at sensitivity in more detail and then will consider how well we can identify odors.

Detecting Odors

Our sense of smell enables us to detect extremely low concentrations of some odorants. The **detection threshold** for odors is the lowest concentration at which an odorant can be detected. One method for measuring detection thresholds is the **forced-choice method**, in which participants are presented with blocks of two trials—one trial contains a weak odorant and the other, no odorant. The participant's task is to indicate which trial has a stronger smell. The threshold is determined by measuring the concentration that results in a correct response on 75 percent of the trials (50 percent would be chance performance).

Table 16.3 lists thresholds for a number of substances. It is notable that there is a very large range of thresholds. T-butyl mercaptan, the odorant that is added to natural gas to warn people of gas leaks, can be detected in very small concentrations of less than 1 part per billion in air. In contrast, to detect the vapors of acetone (the main component of nail polish remover), the concentration must be 15,000 parts per billion, and for the vapor of methanol, the concentration must be 141,000 parts per billion.

Identifying Odors

One of the more intriguing facts about odors is that even though humans can *discriminate* millions or perhaps trillions of different odors, they often find it difficult to accurately *identify* specific odors. For example, when people are presented with the odors of familiar substances such as mint, bananas, and motor oil, they can easily tell the difference between them. However, when they are asked to *identify* the substance associated with the odor, they are successful less than half the time (Desor & Beauchamp, 1974; Engen & Pfaffmann, 1960). However, when people are trained in identifying odors by being told the names of substances when they first smell them and then being reminded of the correct names if they fail to name them correctly on subsequent presentations, they can eventually identify 98 percent of the substances (Desor & Beauchamp, 1974).

One of the amazing things about odor identification is that knowing the correct label for the odor actually seems to transform our perception into that odor. I had this experience a number of years ago when sampling the drink *aquavit* with some friends. Aquavit has a very interesting but difficult to identify smell. Odors such as "anise," "orange," and "lemon" were proposed as we tried to identify its smell, but it wasn't until someone turned the bottle around and read the label on the back that the truth became known: "Aquavit (Water of Life) is the Danish national drink—a delicious, crystal-clear spirit distilled from grain, with a slight taste of caraway." When we heard the word *caraway*, the previous hypotheses of anise, orange, and lemon were transformed into caraway. Thus, when we have trouble identifying odors, this trouble may occur not because of a deficiency in our olfactory system, but from an inability to retrieve the odor's name from our memory (Cain, 1979, 1980).

Table 16.3 Human Odor Detection Thresholds

COMPOUND	ODOR THRESHOLD IN AIR (PARTS PER BILLION)
Methanol	141,000
Acetone	15,000
Formaldehyde	870
Menthol	40
T-butyl mercaptan	0.3

Source: Devos et al., 1990.

DEMONSTRATION | Naming and Odor Identification

To demonstrate the effect of naming substances on odor identification, have a friend collect a number of familiar objects for you and, without your looking, try to identify the odors your friend presents. You will find that you can identify some but not others, but when your friend tells you the answers for the ones you were unable to identify correctly, you will wonder how you could have failed to identify such a familiar smell. Don't blame your mistakes on your nose; blame them on your memory.

Individual Differences in Olfaction

We noted earlier that there are people with anosmia who have lost their sense of smell (p. 389). There are also genetic conditions which cause selective losses of some smells. For example, a section of the human chromosome is associated with receptors that are sensitive to the chemical β-ionone, which is often added to foods and beverages to add a pleasant floral note. Individuals sensitive to β-ionone describe paraffin with low concentrations of β-ionone added as "fragrant" or "floral," whereas individuals with less sensitivity to β-ionone describe the same stimulus as "sour," "pungent," or "acid" (Jaeger et al., 2013). Genetically caused variation in sensitivity occurs for many other chemicals, as well, leading to the idea that everyone experiences his or her own unique "flavor world" (McRae et al., 2013).

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Another example of individual differences in smell is that the smell of the steroid androsterone, which is derived from testosterone, is described negatively ("sweaty," "urinous") by some people, positively by some people ("sweet," "floral"), and as having no odor by others (Keller et al., 2007). Or consider the fact that after eating asparagus some people's urine takes on a smell that has been described as sulfurous, much like cooked cabbage (Pelchat et al., 2011). Some people, however, can't detect this smell.

As noted at the beginning of the chapter, decreases in olfaction is one of the symptoms of the viral infection COVID-19. In addition, it is a predictor of Alzheimer's disease.

Loss of Smell in COVID-19 and Alzheimer's Disease

The recent COVID-19 pandemic, which as I'm writing this in the fall of 2020 is still raging throughout the world, has, among its symptoms, a loss of taste and smell in a majority of patients (Joffily et al., 2020; Sutherland, 2020). The reason for this loss is under intensive investigation.

One explanation that has been proposed is that COVID molecules attach to an enzyme called ACE2 that is found in the intestines, lungs, arteries, and heart, and which has recently been found in the nose. **Figure 16.11** shows that ACE2 is found on the surface of sustentacular cells, which provide metabolic and structural support to the olfactory sensory neurons (Bilinska et al., 2020). It has been proposed, therefore, that COVID-19 causes loss of smell not by directly attacking sensory neurons but by affecting their supporting cells. Exactly how this causes a loss of smell is still being investigated.

The importance of the COVID-induced loss of smell for diagnostic purposes is that it is so common in people with COVID that some researchers have recommended loss of smell as a diagnostic test because it may be a more reliable indicator of the disease than fever or other symptoms (Sutherland, 2020).

Loss of smell is also associated with Alzheimer's disease (AD), a serious loss of memory and other cognitive functions that is often preceded by mild cognitive impairment (MCI), which has affected 50 million people worldwide (Bathini et al., 2019). But an important difference between the olfactory losses associated with AD and COVID-19 is that in AD the loss of olfaction begins occurring decades before the occurrence of clinical symptoms such as memory loss and difficulties in reasoning (Bathini et al., 2019; Devanand et al., 2015). This is shown in **Figure 16.12**, which tracks the progression of the loss of cognition that is the primary symptom of AD (purple curve) and the progression of "biomarkers" associated with AD (Bathini et al., 2019). Notice that the curves for the biomarkers start rising much earlier than the curve for the loss of cognition. The fastest biomarker curve is for Amyloid B (red curve), which is associated with formation of plaques in the brain, and the next-fastest curve is for loss of olfaction (dashed curve).

Abnormal olfactory functioning rises very rapidly during the preclinical phase (yellow shading), and is very high before symptoms of MCI and Alzheimer's begin appearing. This property has led to the proposal that measuring olfactory function is a way to achieve early diagnosis of Alzheimer's, which, in turn, would make it possible to start treatment earlier. (Although there is no cure for AD, treatments are being developed that may slow the development of clinical symptoms.)

Another difference between olfactory loss in AD and in COVID-19 is that the olfactory system may suffer from more widespread attack in AD. There is evidence that AD attacks not only the olfactory bulb, but more central structures, as well. The key conclusion is that the olfactory system appears to be much more sensitive than the visual system or auditory system to neural dysfunction. Thus, although some visual loss precedes AD symptoms, the loss of olfactory function is the key sensory biomarker for predicting development of AD.

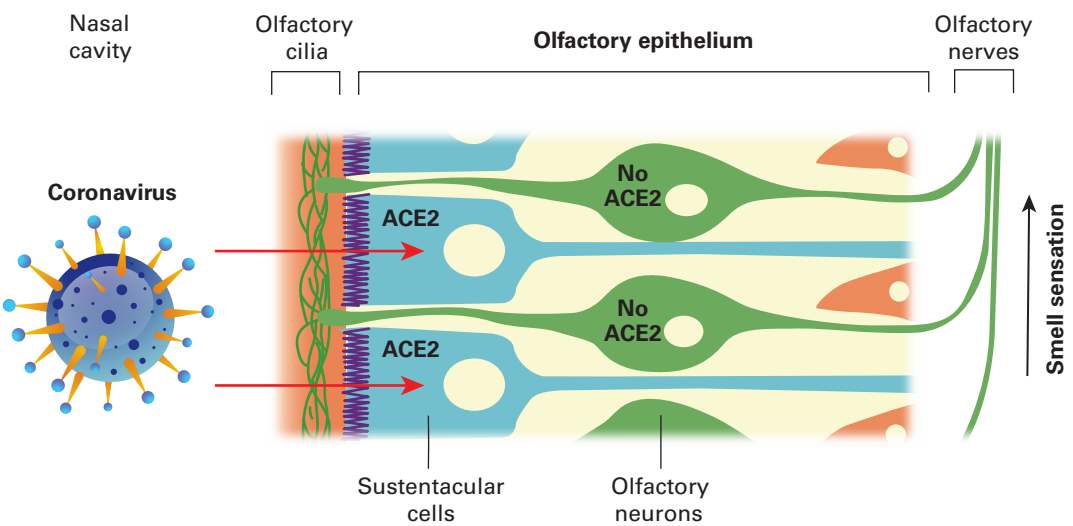

Figure 16.11 Current research on the coronavirus indicates that it attaches to an enzyme, ACE2, which is found in sustentacular cells, which support the olfactory neurons.

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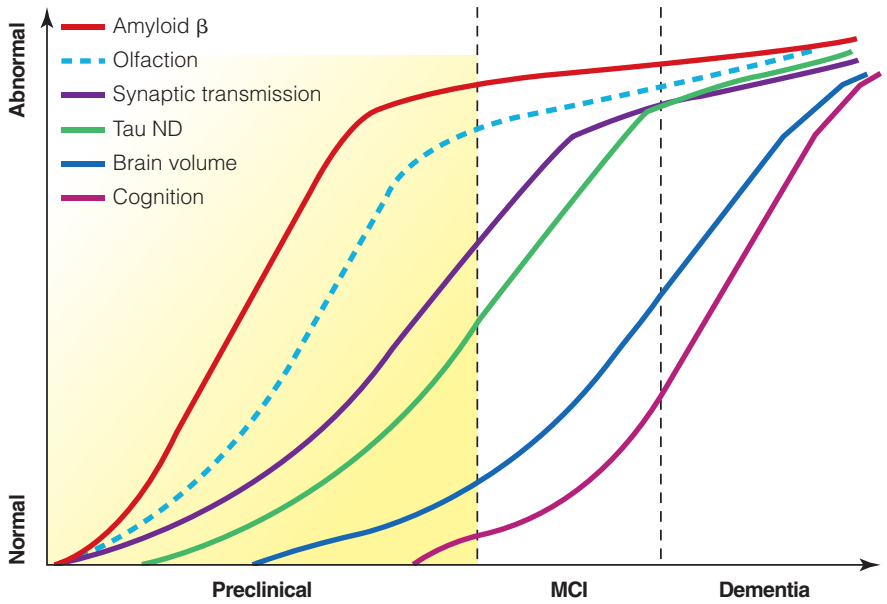

Figure 16.12 Biomarkers in the progression of dementia associated with Alzheimer's disease. The purple line plots the progression of cognitive decline over time. The dashed line plots the progression of loss of olfaction, which precedes cognitive decline. The area shaded yellow indicates the preclinical stage, in which there are no symptoms of cognitive decline. (From Bathini et al., 2019)

A related finding is that loss of olfaction is also associated with a higher risk of death. Jayant Pinto and coworkers (2014) found that in a group of older adults (57–87 years old), who were representative of the general U.S. population, people with anosmia (loss of smell) were three times more likely to die within five years than people with normal smell.

16.7 Analyzing Odorants: The Mucosa and Olfactory Bulb

We have, so far, been describing the functions of olfaction and the experiences that occur when olfactory stimuli, molecules in the air, enter the nose. We now consider the question of how the olfactory system knows what molecules are entering the nose. The first step toward answering this question is to consider some of the difficulties facing researchers who are searching for connections between molecules and perception.

The Puzzle of Olfactory Quality

Although we know that we can discriminate among a huge number of odors, research to determine the neural mechanisms behind this ability is complicated by difficulties in establishing a system to bring some order to our descriptions of odor quality. Such systems exist for other senses. We can describe visual stimuli in terms of their colors and can relate our perception of color to the physical property of wavelength. We can describe sound stimuli as having different pitches and relate these pitches to the physical property of frequency. Creating a way to organize odors and to relate odors to physical properties of molecules, however, has proven extremely difficult.

One reason for the difficulty is that we lack a specific language for odor quality. For example, when people smell the chemical α-ionone, they usually say that it smells like violets. This description, it turns out, is fairly accurate, but if you compare α-ionone to real violets, they smell different. The perfume industry's solution is to use names such as "woody violet" and "sweet violet" to distinguish between different violet smells, but this hardly solves the problem we face in trying to determine how olfaction works.

Another difficulty in relating odors to molecular properties is that some molecules that have similar structures can smell different (**Figure 16.13a**), and molecules that have very different structures can smell similar (**Figure 16.13b**). But things really become challenging when we consider the kinds of odors we routinely encounter in the environment, which consist of mixtures of many chemicals. Consider, for example, that when you walk into the kitchen and smell freshly brewed coffee, the coffee aroma is created by more than 100 different molecules. Although

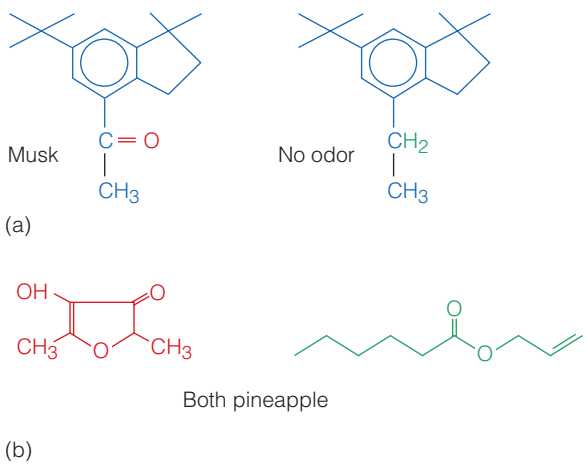

Figure 16.13 (a) Two molecules that have the same structure, but one smells like musk and the other is odorless. (b) Two molecules with different structures but similar odors.

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individual molecules may have their own odors, we don't perceive the odors of individual molecules; we perceive "coffee."

The feat of perceiving "coffee" becomes even more amazing when we consider that odors rarely occur in isolation. Thus, the coffee odor from the kitchen might be accompanied by the smells of bacon and freshly squeezed orange juice. Each of these has its own tens or hundreds of molecules, yet somehow the hundreds of different molecules that are floating around in the kitchen become perceptually organized into smells that refer to three different sources: *coffee*, *bacon*, and *orange juice* (**Figure 16.14**). Sources of odors such as *coffee*, *bacon*, and *orange juice*, as well as nonfood sources such as *rose*, *dog*, and *car exhaust*, are called **odor objects**. Our goal, therefore, is to explain not just how we smell different odor qualities, but how we identify different odor objects.

Perceiving odor objects involves olfactory processing that occurs in two stages. The first stage, which takes place at the beginning of the olfactory system in the *olfactory mucosa* and *olfactory bulb*, involves *analyzing*. In this stage, the olfactory system analyzes the different chemical components of odors and transforms these components into neural activity at specific places in the olfactory bulb (**Figure 16.15**). The second stage, which takes place in the olfactory cortex and beyond, involves *synthesizing*.

Figure 16.14 Hundreds of molecules from the coffee, orange juice, and bacon are mixed together in the air, but the person just perceives "coffee," "orange juice," and "bacon." This perception of three odor objects from hundreds of intermixed molecules is a feat of perceptual organization.

In this stage, the olfactory system synthesizes the information about chemical components received from the olfactory bulb into representations of odor objects. As we will see, it has been proposed that this synthesis stage involves learning and memory. But let's start at the beginning, when odorant molecules enter the nose and stimulate receptors on the olfactory mucosa.

The Olfactory Mucosa

The **olfactory mucosa** is a dime-sized region located on the roof of the nasal cavity just below the **olfactory bulb** (**Figure 16.15a**). Odorant molecules are carried into the nose in an air stream (blue arrows), which brings these molecules into contact with the mucosa. **Figure 16.15b** shows the **olfactory receptor neurons (ORNs)** that are located in the mucosa (colored parts) and the supporting cells (tan area).

Just as the rod and cone receptors in the retina contain visual pigment molecules that are sensitive to light, the olfactory receptor neurons in the mucosa are dotted with molecules called **olfactory receptors** that are sensitive to chemical odorants (**Figure 16.15c**). One parallel between visual pigments and olfactory receptors is that they are both sensitive to a specific range of stimuli. Each type of visual pigment is sensitive to a band of wavelengths in a particular region of the visible spectrum (see Figure 9.13 page 205), and each type of olfactory receptor is sensitive to a narrow range of odorants.

However, an important difference between the visual system and the olfactory system is that while there are only four different types of visual pigments (one rod pigment and three cone pigments), there are about 400 different types of olfactory receptors, each sensitive to a particular group of odorants. The discovery that there are 350 to 400 types of olfactory receptors in the human and 1,000 types in the mouse was made by Linda Buck and Richard Axel (1991), who received the 2004 Nobel Prize in Physiology and Medicine for their research on the olfactory system (also see Buck, 2004).

The large number of olfactory receptor types increases the challenges in understanding how olfaction works. One thing that makes things slightly simpler is another parallel with vision: Just as a particular rod or cone receptor contains only one type of visual pigment, a particular olfactory receptor neuron (ORN) contains only one type of olfactory receptor.

How Olfactory Receptor Neurons Respond to Odorants

Figure 16.16a shows the surface of part of the olfactory mucosa. The circles represent ORNs, with two types of ORNs highlighted in red and blue. Remember that there are 400 different types of ORNs in the mucosa in humans. There are about 10,000 of each type of ORN, so the mucosa contains millions of ORNs.

The first step in understanding how we perceive different odorants is to ask how this array of millions of ORNs that blanket the olfactory mucosa respond to different odorants. One way this question has been answered is by using a technique called *calcium imaging*.

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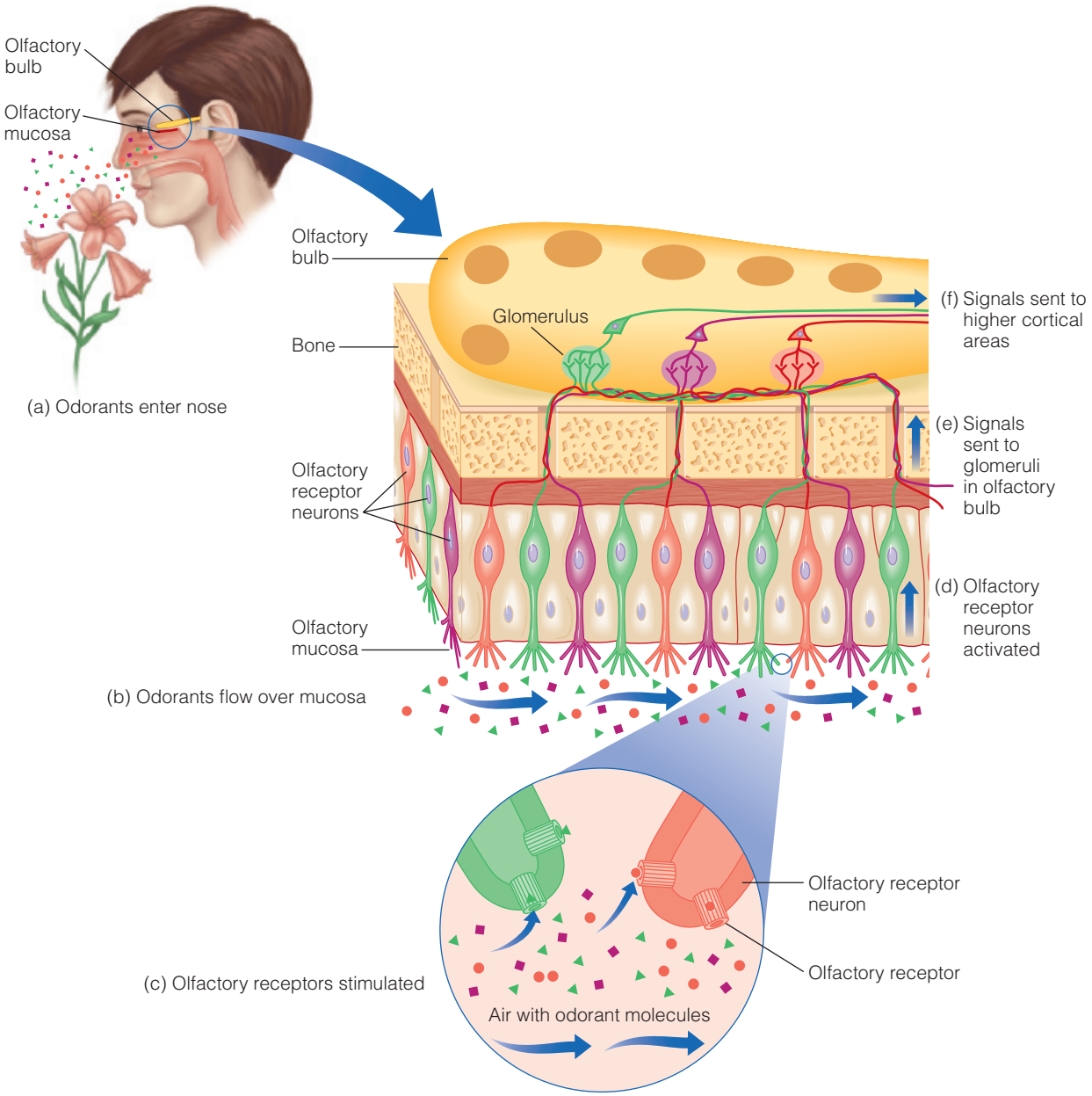

Figure 16.15 The structure of initial structures in the olfactory system. (a) Odorant molecules enter the nose, and then (b) flow over the olfactory mucosa, which contains 350 different types of olfactory receptor neurons (ORNs). (c) Stimulation of receptors in the ORNs (d) activates the ORNs. Three types of ORNs are shown here, indicated by different colors. Each type has its own specialized receptors. (e) Signals from the ORNs are then sent to glomeruli in the olfactory bulb, and then (f) to higher cortical areas.

METHOD | Calcium Imaging

When an olfactory receptor responds, the concentration of calcium ions (Ca++) increases inside the OR. Calcium imaging measures this increase in calcium ions by soaking olfactory neurons in a chemical that causes the ORN to fluoresce with a green glow when exposed to ultraviolet (380 nm) light. This green glow can be used to measure how much Ca++ had entered the neuron because *increasing* Ca++ inside the neuron *decreases* the glow. Thus, measuring the decrease in fluorescence indicates how strongly the ORN is activated.

Bettina Malnic and coworkers (1999) determined the response to a large number of odorants using calcium imaging. The results for a few of her odorants are shown in **Figure 16.17**, which indicates how 10 different ORNs are activated by each odorant. (Remember that each ORN contains only one type of olfactory receptor.)

The response of individual receptors is indicated by the circles in each column. Reading down the columns indicates that each of the receptors, except 19 and 41, responds to some odorants but not to others. The pattern of activation for each odorant, which is indicated by reading across each

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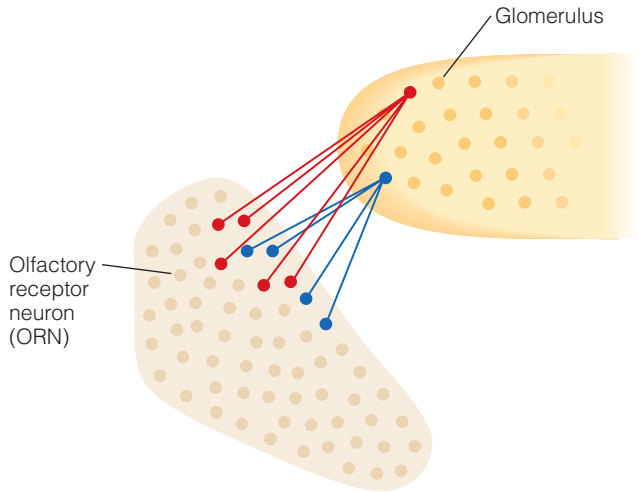

Figure 16.16 (a) A portion of the olfactory mucosa. The mucosa contains 400 types of ORNs and about 10,000 of each type. The red circles represent 10,000 of one type of ORN, and the blue circles, 10,000 of another type. (b) All ORNs of a particular type send their signals to one or two glomeruli in the olfactory bulb.

row, is called the odorant's **recognition profile**. For example, the recognition profile of octanoic acid is weak firing of ORN 79 and strong firing of ORNs 1, 18, 19, 41, 46, 51, and 83, whereas the profile for octanol is strong firing of ORNs 18, 19, 41, and 51.

From these profiles, we can see that each odorant causes a different pattern of firing across ORNs. Also, odorants that have similar structures (shown on the right in Figure 16.17), such as octanoic acid and nonanoic acid, often have similar profiles. We can also see, however, that this doesn't always occur (compare the patterns for bromohexanoic acid and bromooctanoic acid, which also have similar structures).

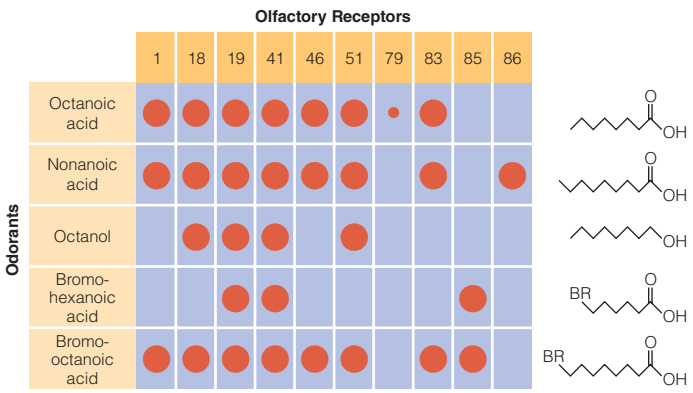

Figure 16.17 Recognition profiles for some odorants. Large dots indicate that the odorant causes a high firing rate for the receptor listed along the top; a small dot indicates a lower firing rate for the receptor. The structures of the compounds are shown on the right.
(Adapted from Malnic et al., 1999)

Remember that one of the puzzling facts about odor perception is that some molecules have similar structures but smell different (Figure 16.13a). When Malnic compared such molecules, she found that these molecules had different recognition profiles. For example, octanoic acid and octanol differ only by one oxygen molecule, but the smell of octanol is described as "sweet," "rose," and "fresh," whereas the smell of octanoic acid is described as "rancid," "sour," and "repulsive." This difference in perception is reflected in their different profiles. Although we still can't predict which smells result from specific patterns of response, we do know that when two odorants smell different, they usually have different profiles.

The idea that an odorant's smell can be related to different response profiles is similar to the trichromatic code for color vision that we described in Chapter 9 (see page 204). Remember that each wavelength of light is coded by a different pattern of firing of the three cone receptors, and that a particular cone receptor responds to many wavelengths. The situation for odors is similar—each odorant is coded by a different pattern of firing of ORNs, and a particular ORN responds to many odorants. What's different about olfaction is that there are 350–400 different types of ORNs, compared to just three cone receptors for vision.

The Search for Order in the Olfactory Bulb

Activation of receptors in the mucosa causes electrical signals in the ORNs that are distributed across the mucosa. These ORNs send signals to structures called **glomeruli** in the olfactory bulb. **Figure 16.16b** illustrates a basic principle of the relationship between ORNs and glomeruli: All of the ORNs of a particular type send their signals to just one or two glomeruli, so each glomerulus collects information about the firing of a particular type of ORN.

This targeting of specific areas of the olfactory bulb by certain receptors creates different patterns of olfactory bulb activation for different odorants. **Figures 16.18** and **16.19**, which are based on measurements of rat olfactory bulb activation using two different techniques (which we won't describe), both show that different chemicals result in different patterns of activity in the olfactory bulb.

Figure 16.18 shows that two different types of compounds, carboxylic acids and aliphatic alcohols, activate different areas on the olfactory bulb, and that as the length of the carbon chain for each compound increases, the area of activation moves to the left. Figure 16.19 also shows that different odorants cause different patterns of activation.

The different patterns for different odorants create a map of odorants in the olfactory bulb that it is based on molecular features of odorants such as carbon chain length or functional groups. These maps have been called **chemotopic maps** (Johnson & Leon, 2007; Johnson et al., 2010; Murthy, 2011), **odor maps** (Restrepo et al., 2009; Soucy et al., 2009; Uchida et al., 2000), and **odotoptic maps** (Nikonov et al., 2005).

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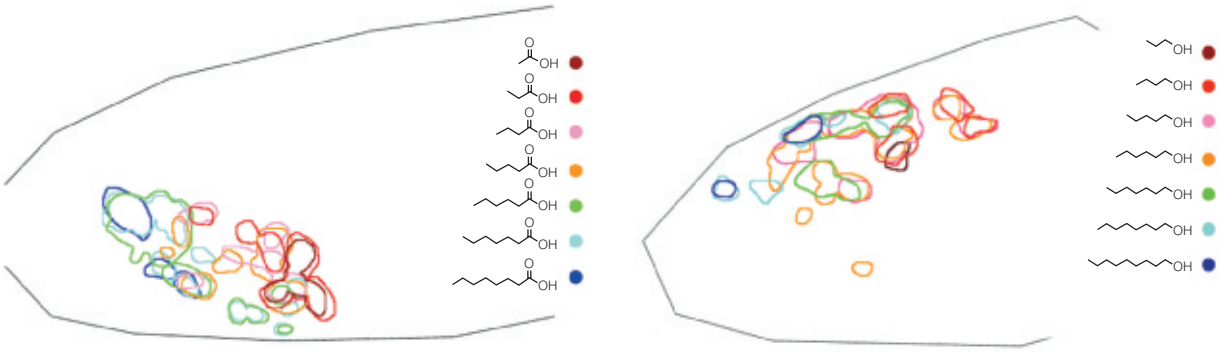

(a) Carboxylic acids (b) Aliphatic alcohols

Figure 16.18 Areas in the rat olfactory bulb that are activated by various chemicals: (a) a series of carbolic acids; (b) a series of aliphatic alcohols. (From Uchida et al., 2000)

The idea that odorants with different properties create a map on the olfactory bulb is similar to the situation we have described for the other senses. There is a retinotopic map for vision, in which locations on the retina are mapped on the visual cortex (p. 75); a tonotopic map for hearing, in which frequencies are mapped onto various structures in the auditory system (p. 278); and a somatotopic map for the cutaneous senses, in which locations on the body are mapped onto the somatosensory cortex (p. 362).

Research on the olfactory map has just begun, however, and much remains to be learned about how odors are represented in the olfactory bulb. Based on what has been discussed so far, it is clear that odorants are at least crudely mapped on the olfactory bulb based on their chemical properties. However, we are far from creating a map based on perception. This map, if it exists, will be a map of different odor experiences arranged on the olfactory bulb (Arzi & Sobel, 2011). But the olfactory bulb represents an early stage of olfactory processing and is not where perception occurs. To understand olfactory perception, we need to follow the output of the olfactory bulb to the olfactory cortex.

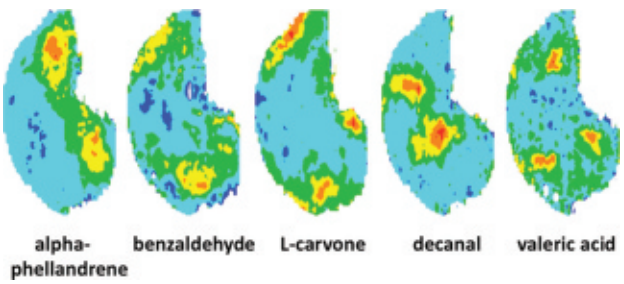

Figure 16.19 Patterns of activation in the rat olfactory bulb for five different odorants. Yellow and red areas indicate areas of high activation compared to activation caused by exposure to air. Each odorant causes a distinctive pattern of activation. (Courtesy of Michael Leon)

TEST YOURSELF 16.2

1. Why is it inaccurate to describe human olfaction as microsmatic?
2. What is the difference between detecting odors and identifying odors?
3. How well can people identify odors? What is the role of memory in identifying odors?
4. Describe some genetically determined individual differences in odor perception. What are some of the consequences of losing the ability to smell?
5. How is olfaction affected by COVID-19 and Alzheimer's disease? Why is it important that loss of olfactory function precedes the main symptoms of AD by many years?
6. Why has it been difficult to organize odors and relate odors to physical properties of molecules?
7. What is an odor object? What are the two stages for perceiving an odor object?
8. Describe the following components of the olfactory system: the olfactory receptors, the olfactory receptor neurons, the olfactory bulb, and the glomeruli. Be sure you understand the relation between olfactory receptors and olfactory receptor neurons, and between olfactory receptor neurons and glomeruli.
9. How do olfactory receptor neurons respond to different odorants, as determined by calcium imaging? What is an odorant's recognition profile?
10. Describe the evidence that there is a chemotopic map on the olfactory bulb. What is the difference between a chemotopic map and a perceptual map?

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16.8 Representing Odors in the Cortex

To begin our discussion of how odors are represented in the cortex, let's look at where signals are transmitted when they leave the olfactory bulb. **Figure 16.20a** shows the location of the two main olfactory areas: (1) the piriform cortex (PC), which is the primary olfactory area, and (2) the orbitofrontal cortex, which is the secondary olfactory area. **Figure 16.20b** shows the olfactory system as a flow diagram and adds the amygdala, which is involved in determining emotional reactions not only to smell but also to faces and pain. We begin by considering the piriform cortex.

How Odorants Are Represented in the Piriform Cortex

So far in our journey through the olfactory system, progressing from the olfactory neurons to the olfactory bulb, order has prevailed. Odors that smell different cause different patterns of firing of olfactory receptors (Figure 16.17). Moving to the olfactory bulb, different chemicals cause activity in specific areas, which has led to the proposal of odotopic maps (Figures 16.18 and 16.19).

But when we move up to the piriform cortex (PC), something surprising happens: The map vanishes! Odorants that caused activity in specific locations in the olfactory bulb now cause widespread activity in the PC, and there is overlap between the activity caused by different odorants.

This shift in organization from the olfactory bulb to the PC is illustrated in a study by B. F. Osmanski and coworkers (2014), who used a technique called *functional ultrasound imagery*, which, like fMRI, determines brain activation by measuring changes in blood flow. **Figure 16.21a** shows that hexanal and pentyl acetate cause different patterns of activity in the rat olfactory bulb. **Figure 16.21b** shows that hexanal and pentyl acetate cause activity throughout the entire PC.

This widespread activity in the PC has also been demonstrated by recording from single neurons. **Figure 16.22** shows the results of an experiment by Robert Rennaker and coworkers (2007), who used multiple electrodes to measure neural responding in the PC. Figure 16.22 shows that isoamyl acetate causes activation across the cortex. Other compounds also cause widespread activity, and there is substantial overlap between the patterns of activity for different compounds.

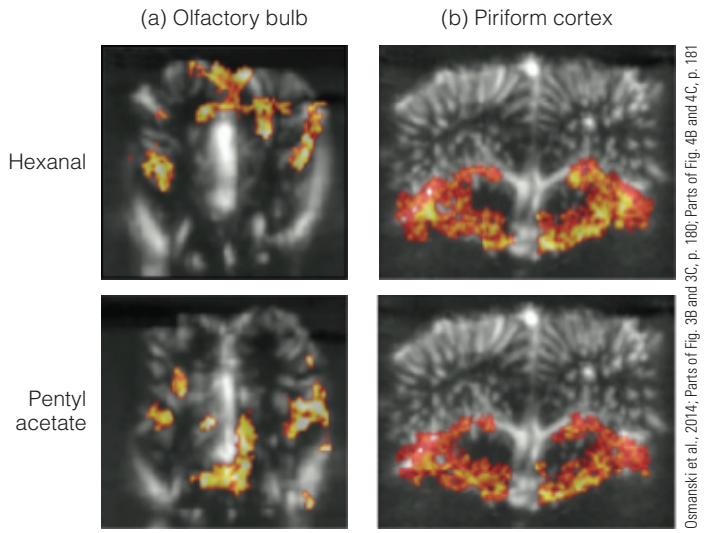
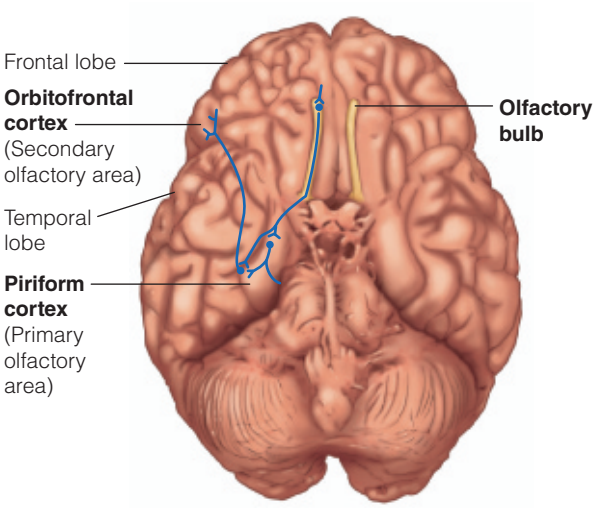

(a) Olfactory bulb
(b) Piriform cortex
Hexanal
Pentyl acetate
Osmanski et al., 2014; Parts of Fig. 3B and 3C, p. 180; Parts of Fig. 4B and 4C, p. 181

Figure 16.21 Response of the rat's (a) olfactory bulb and (b) piriform cortex to hexanal and pentyl acetate measured by functional ultrasound scanning. See text for details. (From Osmanski et al., 2014)



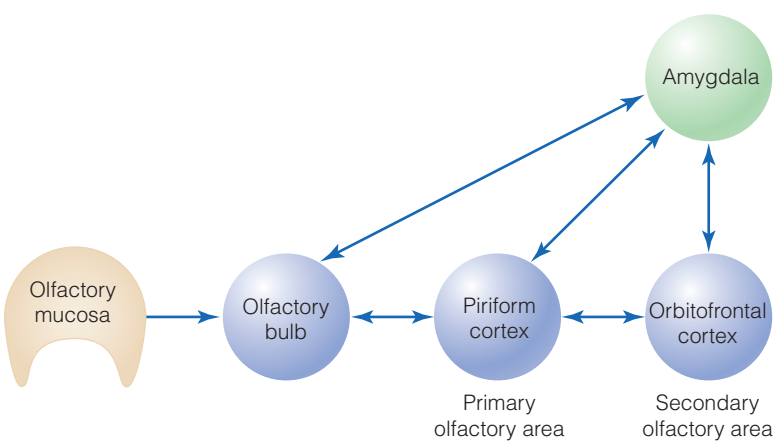


Figure 16.20 (a) The underside of the brain, showing the neural pathways for olfaction. On the left side, the temporal lobe has been deflected to expose the olfactory area. (b) Flow diagram of the pathways for olfaction.
[(a) Adapted from Frank & Rabin, 1989; (b) adapted from Wilson & Stevenson, 2006]

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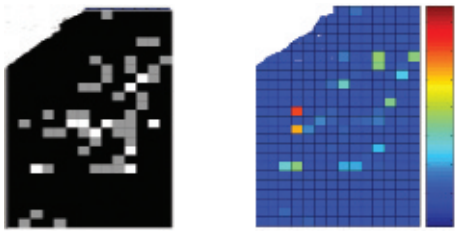

(a) Electrode placements (b) Activation by isoamyl acetate

Figure 16.22 (a) Recording sites used by Rennaker and coworkers (2007) to determine activity of neurons in the piriform cortex of the rat. (b) The pattern of activation caused by isoamyl acetate.

These results show that the orderly activation pattern in the olfactory bulb no longer exists in the piriform cortex. This occurs because the projection from the olfactory bulb is scattered, so activity associated with a single chemical is spread out over a large area. Things become even more interesting when we ask what the activation pattern might look like for an odor object such as *coffee*.

How Odor Objects Are Represented in the Piriform Cortex

We can appreciate how complicated things become for odor objects by imagining what the pattern of activation would be for *coffee*, which contains a hundred different chemical components. Not only will the pattern be very complicated, but if you are smelling a particular odor for the first time, this raises the question of how the olfactory system is able to determine the identity of this "mystery odor" based on the information in this first-time response. Some researchers have answered this question by drawing a parallel between recognizing odors and experiencing memories.

Figure 16.23 indicates what happens when a memory is formed. When a person witnesses an event, a number of neurons are activated (**Figure 16.23a**). At this point, the memory for the event isn't completely formed in the brain; it is fragile and can be easily forgotten or can be disrupted by trauma, such as a blow to the head. But connections begin forming between the neurons that were activated by the event (**Figure 16.23b**), and after these connections are formed (**Figure 16.23c**), the memory is stronger and more resistant to disruption. Formation of stable memories thus involves a process in which linkages are formed between a number of neurons.

Applying this idea to odor perception, it has been proposed that formation of odor objects involves learning, which links together the scattered activations that occur for a particular object. We can see how this works by imagining that you are smelling the odor of a flower for the first time. The odor of this flower, just like the odors of coffee and other substances, is created by a large number of chemical compounds (**Figure 16.24a**). These chemical components first activate the olfactory receptors in the mucosa and then create a pattern of activation on the olfactory bulb that is shaped by the chemotopic map. This pattern occurs any time the flower's odor is presented (**Figure 16.24b**). From the research described above, we know that signals from the olfactory bulb are transformed into a scattered pattern of activation in the piriform cortex (**Figure 16.24c**).

Because this is the first time you have ever experienced the flower's odor, the activated neurons aren't associated with each other. This is like the neurons that represent a new memory, which aren't yet linked (see Figure 16.23a). At this point you are likely to have trouble identifying the odor and might confuse it with other odors. But after a number of exposures to the flower, which cause the same activation pattern to occur over and over, neural connections form, and the neurons become associated with each other (**Figure 16.24d**). Once this occurs, a pattern of activation has been created that represents the flower's odor. Thus, just as a stable memory becomes established when neurons become linked, odor objects become formed when experience with an odor causes neurons in the piriform cortex to become linked. According to this idea, when the person in Figure 16.14 walks into the kitchen, the activation caused by the hundreds of molecules in the air become three linked networks of activation in the PC that stand for *coffee*, *orange juice*, and *bacon*.

The idea that learning plays an important role in perceiving odors is supported by research. For example, Donald Wilson (2003) measured the response of neurons in the rat's piriform cortex to two odorants: (1) a *mixture* of isoamyl acetate, which has a banana-like odor, and peppermint and (2) the *component* isoamyl acetate alone. Wilson was interested in how well the rat's neurons could tell the difference between the mixture and the component after the rat had been exposed to the mixture.

Wilson presented the mixture to the rat for either a brief exposure (10 seconds or about 20 sniffs) or a longer exposure (50 seconds or about 100 sniffs) and, after a short pause, measured the response to the *mixture* and to the *component*. Following 10 seconds of sniffing, the piriform neurons responded similarly to the mixture and to the component. However, following 50 seconds of sniffing, the neurons fired more rapidly to the component. Thus, after 100 sniffs of the mixture, the neurons became able to tell the difference between the mixture and the component. Similar experiments

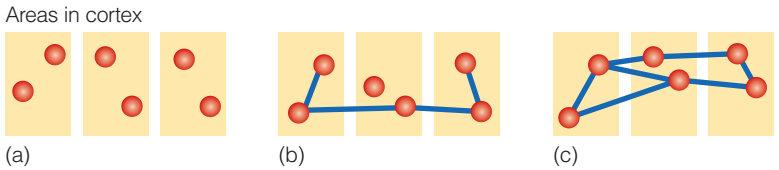

Figure 16.23 A model of how memories are formed in the cortex. (a) Initially, incoming information activates a number of areas in the cortex. The rectangles are different cortical areas. Red circles are activated areas. (b) As time passes, the neural activity is replayed, which creates connections between activated areas. (c) Eventually, the activated areas for a particular memory are linked, which stabilizes the memory.

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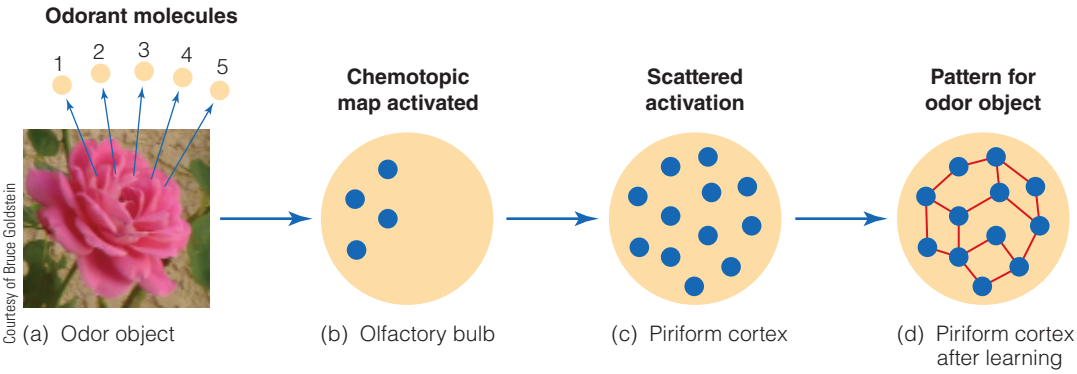

Figure 16.24 Memory mechanism for forming representations of the flower's odor. See text for details.

measuring responses of neurons in the olfactory bulb did not show this effect.

Wilson concluded from these results that, given enough time, neurons in the piriform cortex can learn to discriminate between different odors, and that this learning may be involved in our ability to tell the difference between different odors in the environment. Numerous other experiments support the idea that a mechanism involving experience and learning is involved in associating patterns of piriform cortex firing with specific odor objects (Choi et al., 2011; Gottfried, 2010; Sosulski et al., 2011; Wilson, 2003; Wilson et al., 2004, 2014; Wilson & Sullivan, 2011).

How Odors Trigger Memories

While memory is involved in identifying odor objects, there is another, different, connection between olfaction and memory. Olfaction can, under some circumstances, *create* memories. This connection between chemical senses and memory was noted by the French author Marcel Proust (1871–1922) in his description of an experience after eating a small lemon cookie called a madeleine:

> The sight of the little madeleine had recalled nothing to my mind before I tasted it... as soon as I had recognized the taste of the piece of madeleine soaked in her decoction of lime-blossom which my aunt used to give me... immediately the old grey house upon the street, where her room was, rose up like a stage set to attach itself to the little pavilion opening on to the garden which had been built out behind it for my parents... and with the house the... square where I used to be sent before lunch, the streets along which I used to run errands, the country roads we took when it was fine. (Marcel Proust, *Remembrance of Things Past*, 1913)

Proust's rather dramatic description of how tasting a cookie unlocked memories he hadn't thought of for years is called the **Proust effect**. This passage captures some characteristics of Proustian memories: (1) Memories were realized not by seeing the cookie but by tasting it; (2) the memory was vivid and transported Proust back to a number of places from his past; and (3) the memory was from Proust's early childhood.

Modern researchers call these Proustian memories **odor-evoked autobiographical memories** (OEAMs), because they are elicited by odors and are memories about events from a person's life story. But OEAMs aren't simply a literary observation. In an early experiment that confirmed and elaborated on the properties of OEAMs hinted at by Proust's observations, Rachel Herz and Jonathan Schooler (2002) had participants describe a personal memory associated with items like Crayola crayons, Coppertone suntan lotion, and Johnson's baby powder. After describing their memory associated with the objects, participants were presented with an object either in visual form (a color photograph) or in odor form (smelling the object's odor) and were asked to think about the event they had described and to rate it on a number of scales. The result was that participants who smelled the odor rated their memories as more emotional than participants who saw the picture. They also had a stronger feeling than the visual group of "being brought back" to the time the memory occurred (also see Willander & Larsson, 2007).

The fact that Proust described a memory from his childhood is no coincidence, because an experiment that collected autobiographical memories from 65- to 80-year-old participants elicited by odors, words, or pictures yielded the results shown in **Figure 16.25** (Larsson & Willander, 2009). Memories elicited by odors were most likely to be for events that occurred in the first decade of life, whereas memories elicited by words were more likely to be for events from the second decade of life. The participants in this experiment also described their odor-evoked memories as being associated with strong emotions and feelings of being brought back in time.

What's happening in the brain during OEAMs? A clue to the answer is that the amygdala, which is involved in creating emotions and emotional memories, is only two synapses from the olfactory nerve, and the hypothalamus, which is involved in storing and retrieving memories, is only three synapses away. It therefore isn't surprising that fMRI brain scans have revealed that odor-evoked memories cause higher activity in the amygdala than word-evoked memories (Arshamian et al., 2013; Herz et al., 2004).

So Proust was onto something when he described how the flavor of a cookie transported him back in time. The research inspired by Proust's observation indicates that there is something special about olfactory memories. It is also important to note that although Proust described "tasting" the madeleine

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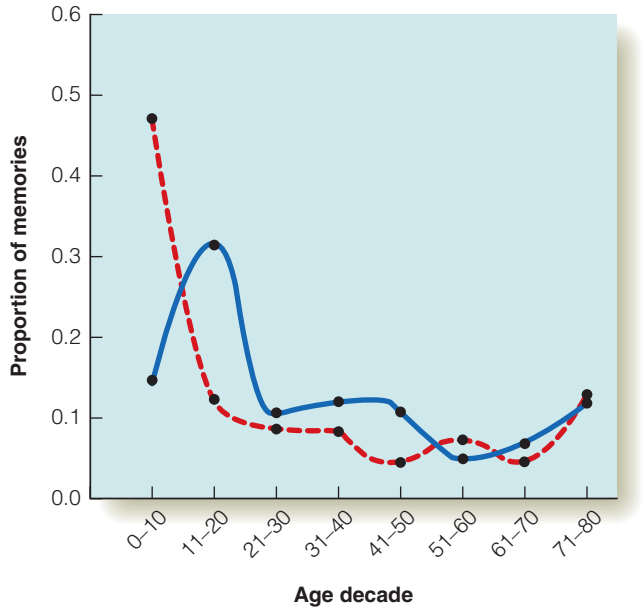

Figure 16.25 Distribution of events associated with odor-cued memories (dashed curve) and word-cued memories (solid curve) over the lifespan. The events retrieved from odor-cued memories peak during the first decade of life, whereas the events retrieved from word-cued memories peak during the second decade.

cookie, he was really describing *flavor*, which is determined by a combination of taste and olfaction.

16.9 The Perception of Flavor

What most people refer to as "taste" when describing their experience of food ("That tastes good, Mom") is usually a combination of taste, from stimulation of the receptors in the tongue, and olfaction, from stimulation of the receptors in the olfactory mucosa. This combination, which is called flavor, is defined as the overall impression that we experience from the combination of nasal and oral stimulation (Lawless, 2001; Shepherd, 2012). You can demonstrate how smell affects flavor with the following demonstration.

DEMONSTRATION | Tasting With and Without the Nose

While pinching your nostrils shut, drink a beverage with a distinctive taste, such as grape juice, cranberry juice, or coffee. Notice both the quality and the intensity of the taste as you are drinking it. (Take just one or two swallows because swallowing with your nostrils closed can cause a buildup of pressure in your ears.) After one of the swallows, open your nostrils, and notice whether you perceive a flavor. Finally, drink the beverage normally with nostrils open, and notice the flavor. You can also do this demonstration with fruits or cooked foods or try eating a jellybean with your eyes closed (so you can't see its color) while holding your nose.

The reason you may have found it difficult to determine what you were drinking or eating when you were holding your nose is that your experience of flavor depends on a combination of taste and olfaction, and by holding your nose, you eliminated the olfactory component of flavor. This interaction between taste and olfaction occurs at two levels: first in the mouth and nose, and then in the cortex.

Taste and Olfaction Meet in the Mouth and Nose

Chemicals in food or drink cause taste when they activate taste receptors on the tongue. But in addition, food and drink release volatile chemicals that reach the olfactory mucosa by following the **retronasal route**, from the mouth through the **nasal pharynx**, the passage that connects the oral and nasal cavities (Figure 16.1). Although pinching the nostrils shut does not close the nasal pharynx, it prevents vapors from reaching the olfactory receptors by eliminating the circulation of air through this channel (Murphy & Cain, 1980). The same thing happens when you have a cold—less airflow means the flavor of foods will be greatly reduced.

The fact that olfaction is a crucial component of flavor may be surprising because the flavors of food seem to be centered in the mouth. It is only when we keep molecules from reaching the olfactory mucosa that the importance of olfaction is revealed. One reason this localization of flavor occurs is because food and drink stimulate tactile receptors in the mouth, which creates **oral capture**, in which the sensations we experience from both olfactory and taste receptors are referred to the mouth (Small, 2008). Thus, when you "taste" food, you are usually experiencing flavor, and the fact that it is all happening in your mouth is an illusion created by oral capture (Todrank & Bartoshuk, 1991).

The importance of olfaction in the sensing of flavor has been demonstrated experimentally by using both chemical solutions and typical foods. In general, solutions are more difficult to identify when the nostrils are pinched shut (Mozell et al., 1969) and are often judged to be tasteless. For example, **Figure 16.26a** shows that the chemical sodium oleate has a strong soapy flavor when the nostrils are open but is judged tasteless when they are closed. Similarly, ferrous sulfate (**Figure 16.26b**) normally has a metallic flavor but is judged predominantly tasteless when the nostrils are closed (Hettinger et al., 1990). However, some compounds are not influenced by olfaction. For example, monosodium glutamate (MSG) has about the same flavor whether or not the nose is clamped (**Figure 16.26c**). In this case, the sense of taste predominates.

Taste and Olfaction Meet in the Nervous System

Although taste and olfactory stimuli occur in close proximity in the mouth and nose, our perceptual experience of their combination is created when they interact in the cortex.

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	Sodium oleate		Ferrous sulfate		MSG	
	Clamped	Open	Clamped	Open	Clamped	Open
Sweet	x		x			
Salty	x				xxxxxxxxx	xxxxxxxx
Sour			xx	x	xxx	xxx
Bitter		x	x		xx	x
Soapy	xx	xxxxxxxxx	x	xx		
Metallic		xx	x	xxxxxxxxx		
Sulfurous				x	x	xx
Tasteless	xxxxxxxx		xxxxxx	x		
Other	x	x	x		x	xxx
	(a)		(b)		(c)	

Figure 16.26 How people described the flavors of three different compounds when they tasted them with their nostrils clamped shut and with their nostrils open. Each X represents the judgment of one person. (From Hettinger et al., 1990)

Figure 16.27 is the diagram of the olfactory pathway from Figure 16.16b (in blue) with the taste pathway added (in orange), showing connections between olfaction and taste (Rolls et al., 2010; Small, 2012). In addition, vision and touch contribute to flavor by sending signals to the amygdala (vision), structures in the taste pathway (touch), and the orbitofrontal cortex (vision and touch).

All of these interactions among taste, olfaction, vision, and touch underscore the multimodal nature of our experience of flavor. Flavor includes not only what we typically call "taste," but also perceptions such as the texture and temperature of food (Verhagen et al., 2004), the color of food (Spence, 2015; Spence et al., 2010), and the sounds of "noisy" foods such as potato chips and carrots that crunch when we eat them (Zampini & Spence, 2010). We will have more to say about the multimodal nature of flavor in the Something to Consider section at the end of the chapter.

Because of this convergence of neurons from different senses, the orbitofrontal cortex contains many **bimodal neurons**, neurons that respond to more than one sense. For example, some bimodal neurons respond to both taste and smell, and others respond to taste and vision. An important property of these bimodal neurons is that they often respond to similar qualities. Thus, a neuron that responds to the taste of sweet fruits would also respond to the smell of these fruits. This means that neurons are tuned to respond to qualities that occur together in the environment. Because of these properties, it has been suggested that the orbitofrontal cortex is a cortical center for detecting flavor and for the perceptual representation of foods (Rolls & Baylis, 1994; Rolls et al., 2010). Other

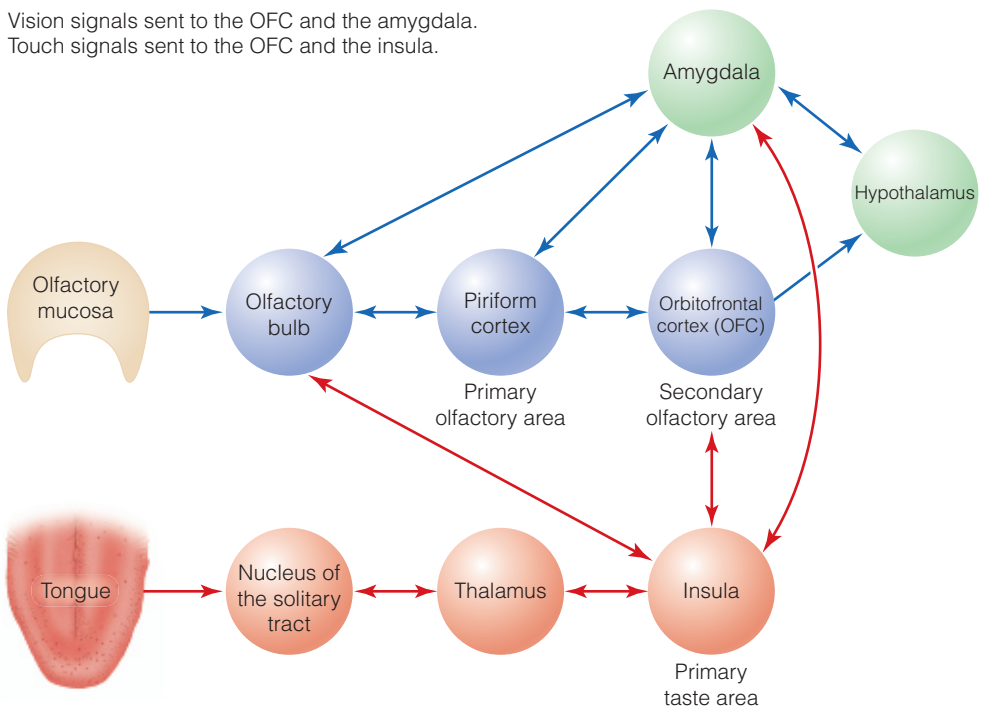

Figure 16.27 Flavor is created by interactions among taste, olfaction, vision, and touch. The olfactory pathway (blue) and taste pathway (red) interact, as signals are sent between these two pathways. In addition, both taste and olfactory pathways send signals to the orbitofrontal cortex (OFC), signals from touch are sent to the taste pathway and the OFC, and signals from vision are sent to the OFC. Also shown are the amygdala, which is responsible for emotional responses and has many connections to structures in both the taste and olfaction pathways and also receives signals from vision, and the hypothalamus, which is involved in determining hunger.

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research has shown that the insula, the primary taste cortex, is also involved in the perception of flavor (de Araujo et al., 2012; Veldhuizen et al., 2010).

But flavor isn't a fixed response that is automatically determined by the chemical properties of food. Although the chemicals in a particular food may always activate the same pattern of ORNs in the mucosa, by the time the signals reach the cortex they can be affected by many different factors, including cognitive factors and the amount of a particular food the person has consumed.

Flavor Is Influenced by Cognitive Factors

What you expect can influence both what you experience and neural responding. This was demonstrated by Hilke Plassmann and coworkers (2008) by having participants in a brain scanner judge the "taste pleasantness" of different samples of wine. Participants were asked to indicate how much they liked five different wines, which were identified by their price. In reality, there were only three wines; two of them were presented twice, with different price labels. The results, for a wine that was labeled either $10 or $90, are shown in **Figure 16.28**. When the wines are presented without labels, the taste pleasantness judgments are the same (**Figure 16.28a**, left bars), but when tasting is preceded by a price label, the "$90 wine" gets a much higher taste rating than the "$10 wine." In addition to influencing the person's judgments, the labels also influence the response of the orbitofrontal cortex, with the $90 wine causing a much large response (**Figure 16.28b**).

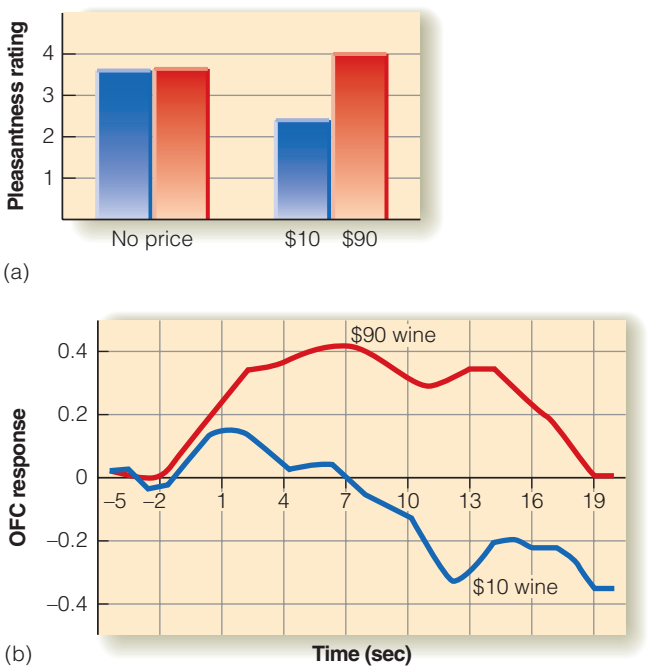

Figure 16.28 Effect of expectation on flavor perception, as indicated by the results of Hilke Plassman and coworkers' (2008) experiment. (a) The red and blue bars indicate ratings given to two presentations of the same wine (although participants didn't know they were the same). The two bars on the left indicate ratings when there were no price labels on the wines. The two bars on the right indicate that the participants give higher "taste pleasantness" ratings when the wine is labeled $90, compared to when it is labeled $10. (b) Responses of the OFC when tasting the wines labeled $10 and $90.

What's happening here is that the response of the orbitofrontal cortex is being determined both by signals that begin with stimulation of the taste and olfactory receptors and by signals created by the person's expectations. In another experiment, participants rated the same odor as more pleasant when it was labeled "cheddar cheese" than when it was called "body odor," and the orbitofrontal cortex response was larger for the cheddar cheese label (de Araujo et al., 2005).

Many other experiments have shown that flavor is influenced by factors in addition to the actual food that is being consumed. The taste of a red frozen strawberry dessert was judged to be 10 percent sweeter and 15 percent more flavorful when it was presented on a white plate compared to on a black plate (Piqueras-Fiszman et al., 2012). The sweetness of café latte was almost doubled when consumed from a blue mug compared to a white mug (Van Doorn et al., 2014). And returning to wine, experiments have shown that perception of the flavor of wine can be influenced not only by information about its price but also by the shape of the wine glass (Hummel et al., 2003).

Flavor Is Influenced by Food Intake: Sensory-Specific Satiety

Have you ever experienced the first few forkfuls of a particular food as tasting much better than the last? Food consumed to satiety (when you don't want to eat any more) is often considered less pleasurable than food consumed when hungry.

John O'Doherty and coworkers (2000) showed that both the pleasantness of a food-related odor and the brain's response to the odor can be influenced by satiety. Participants were tested under two conditions: (1) when hungry and (2) after eating bananas until satiety. Participants in a brain scanner judged the pleasantness of two food-related odors: banana and vanilla. The pleasantness ratings for both were similar before they had consumed any food. However, after eating bananas until satiety, the pleasantness rating for vanilla decreased slightly (but was still positive), but the rating for banana decreased much more and became negative (**Figure 16.29a**). This larger effect on the odor associated with the food eaten to satiety, called sensory-specific satiety, also occurred in the response of the orbitofrontal cortex. The orbitofrontal cortex response decreased for the banana odor but remained the same for the vanilla odor (**Figure 16.29b**). Similar effects also occurred in the amygdala and insula for some (but not all) participants.

The finding that orbitofrontal cortex activity is related to the pleasantness of an odor or flavor can also be stated in another way: The orbitofrontal cortex is involved in determining the *reward value* of foods. Food is more rewarding when you are hungry and becomes less rewarding as food is consumed, until eventually—at satiety—the reward is gone and eating stops.

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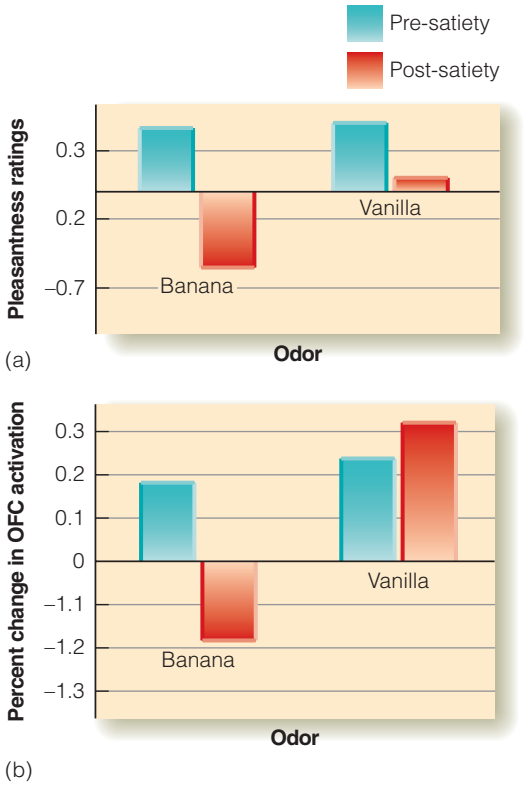

Figure 16.29 Sensory-specific satiety. Results of the O'Doherty et al. (2000) experiment. (a) Pleasantness rating for banana and vanilla odor before eating (left bars) and after eating bananas to satiety (right bars). (b) Response of the orbitofrontal cortex to banana and vanilla odors before and after eating bananas.

These changes in the reward value of flavors are important because just as taste and olfaction are important for warning of danger, they are also important for regulating food intake. Also note in Figure 16.27 that the orbitofrontal cortex sends signals to the hypothalamus, where neurons are found that respond to the sight, taste, and smell of food if hunger is present (Rolls et al., 2010).

What we've learned by considering each of the stages of the systems for taste, olfaction, and flavor is that the purpose of the chemical senses extends beyond simply creating experiences of taste, smell, and flavor. Their purpose is to help guide behavior—avoiding potentially harmful substances, seeking out nutrients, and helping control the amount of food consumed. In fact, even neurons in the olfactory bulb are sensitive to signals the body creates about hunger and satiety. Thus they respond to food odors in the context of signals from the body about how hungry you are.

Does this description of a sense being concerned with behavior sound familiar? You may remember that Chapter 7, "Taking Action," presented a similar message for vision: Although early researchers saw the visual system as being concerned primarily with creating visual experiences, later researchers have argued that the ultimate goal of the visual system is to support taking actions that are necessary for survival (see page 149). The chemical senses have a similar ultimate purpose of guiding and motivating actions required for survival. We eat in order to live, and our experience of flavor helps motivate that eating. (Unfortunately, it should be added, the shutoff mechanisms are sometimes overridden by manufactured foods that are rich in sugar and fat and by other factors, with obesity as an outcome—but that's another story.)

SOMETHING TO CONSIDER:

The Community of the Senses

We live in a world that is not organized as separate senses, like the chapters in a sensation and perception textbook, but exists as a rich tapestry of moving and stationary objects, spaces, sounds, smells, and potentials for action, among other things. This tapestry is decorated with properties like color and shape, pitch and rhythm, rough and smooth textures. All of these things together combine to create our experience of the environment.

For example, consider the bird that just flew past me. It was small, gray with dotted smoothly textured feathers, and a series of rapid flying movements placed it on a shaded tree branch, where it began its song—a series of rapid high-pitched tweets. I perceived this constellation of appearances, behaviors, and sounds as characteristic of this particular bird, and knowing the properties of this bird led me to predict certain things about it. If it had emitted a low-pitched "caw, caw" sound that is normally associated with much larger birds, I would have been extremely surprised. Certain properties—size, sound, movements—go together in certain situations.

But enough about birds. How about something really important, like baseball. You see the pitcher throw the ball. The batter swings and from the loud crack of the bat you know that the ball is most probably going out of the park. But a swing without that sound, followed by the "thwunk" of the ball hitting the catcher's glove, signals a strike. You may not be conscious of it as you're watching the game, but seeing and hearing are working together to provide information about what is happening.

Examples of **multimodal interactions**—interactions that involve more than one sense or quality—are endless, because they are all around us. You propose a toast, clink wine glasses, and the contact between the glasses is signaled by both vision and hearing. As you are talking to someone in a noisy room, hearing them becomes easier if you can see their lips moving as they are speaking to you. You see people dancing to music on TV or on your phone or computer. When you turn off the sound you still see them dancing, but something's missing. With the sound on, their movement not only seems more synchronized, but you may feel like moving yourself. And if you were the one dancing, the modalities of touch and pressure would be added to the music, vision, and action.

Two visual-auditory interactions we discussed in this book are the ventriloquism effect, in which the perceived location of the sound source is determined by vision (see page 306), and the

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McGurk effect, in which seeing a speaker's lips move can affect what sound the listener hears (McGurk effect: see page 343).

But what about taste and smell? They are multimodal when they combine to create flavor. But taste and smell also interact with non-chemical senses in numerous ways. This makes sense, because when we smell something, there's an object involved, such as food on a plate or liquid in a glass. Smell and taste also occur within a particular situation—cooking smells in a kitchen, a smoke alarm signaling smoke in a house, the smell of hot dogs being grilled outside in a park. Here are a few examples of experiments that studied interactions between the chemical senses and the other senses, divided into two types, correspondences and influences.

Correspondences

Correspondences refer to how a property of a chemical sense—taste, olfaction, or flavor—is associated with properties of other senses.

Odors and Tastes Are Associated With Different Pitches and Instruments When participants were presented with odors like almond, cedar, lemon, raspberry, and vanilla and were asked to pick the auditory pitch that matched the odor, pitches were matched to different odors. **Figure 16.30a** indicates that fruits were matched by high pitches, and smells such as smoked, musk, and dark chocolate were matched by lower pitches (Crisinel & Spence, 2012). In a study using taste stimuli, the tastes of citric acid and sucrose were matched to high tones, and coffee and MSG were matched to lower tones (Crisinel & Spence, 2010). This study was titled "As Bitter as a Trombone," because when also asked to match tastes and musical instruments, bitter substances, like caffeine, were more likely to be matched to brass instrument sounds, and sweet substances, like sugar, were more likely to be matched to piano or string sounds (**Figure 16.30b**).

Odors Are Associated With Different Colors When participants sniffed a wide range of odors and picked colors that matched them, they matched odors to specific colors (Maric & Jacquot, 2013). For example, pineapple was associated with red, yellow, pink, orange, and purple, whereas caramel was associated with brown, orange, and pale orange. Wild strawberry odor was matched by red, pink, and purple; "smoked" odor by brown, dark red, black, and gray.

Odors Are Associated With Different Textures When participants judged the texture of fabric while smelling different odors, they judged the fabrics to be slightly softer when smelling a pleasant lemon odor than when smelling an unpleasant animal-like odor (Dematte et al., 2006). Other research has shown that different odors are associated with specific textures. For example, cinnamon and onion odors are associated with rough textures, whereas violet and peppermint are associated with smooth textures (Spector & Maurer, 2012).

Influences

Influences occur when stimuli from one sense affect our perception or performance associated with another sense.

Music Can Influence Flavor Often, the experience of eating at a restaurant or bar is accompanied by background music. While this music may be creating a relaxing mood in a "fine dining" restaurant, or a more upbeat mood in a bar, it may also be affecting the flavor of the food. Felipe Reinoso Carvalho and coworkers (2017) demonstrated this by having participants taste samples of chocolate while listening to two different soundtracks. The soft/smooth track consisted of long, consonant notes (where *consonant* refers to notes that go well together), whereas the hard/rough track had staccato dissonant notes. The results were clear-cut—when participants had eaten the chocolate while listening to the soft/smooth soundtrack they rated it as creamier and sweeter than if eaten during the hard/rough track. This research and other research has shown that music can affect our perception of a food's flavor (Crisinel et al., 2012; Wang & Spence, 2018).

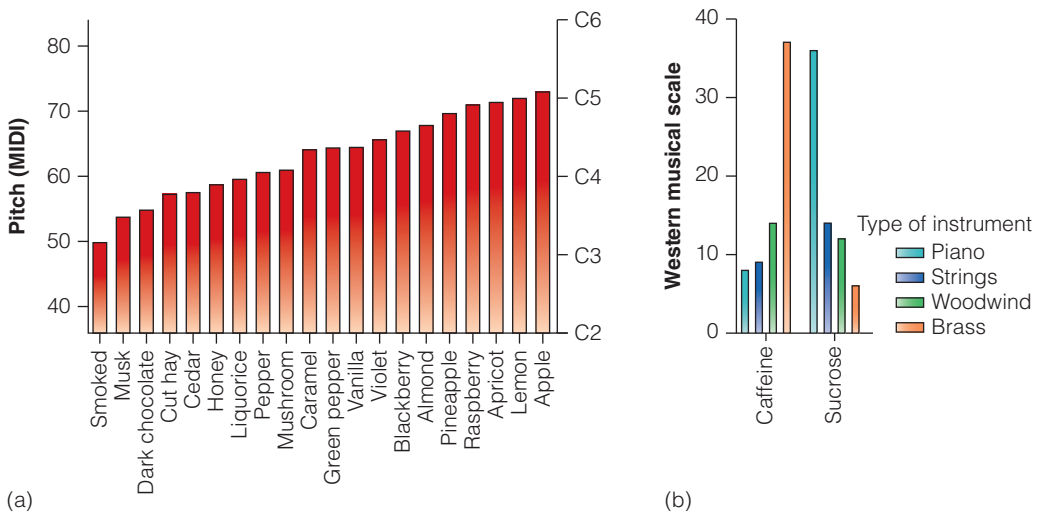

Figure 16.30 (a) Pitches matched to a range of different odors. The vertical axis indicates the western musical scale. There is one octave between C3 and C4 and between C4 and C5. (From Crisinel & Spence, 2012) (b) The heights of the bars indicate the number of participants who matched different instruments to caffeine and sucrose. Note that brass instruments were the main choice as a match for caffeine, whereas piano was the choice for sucrose. (From Crisinel & Spence, 2010)

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Color Can Influence Flavor Participants perceive a cherry-flavored drink as orange-flavored if it is colored orange (DuBose et al., 1980) and rate a strawberry-flavored drink as less pleasant if it is colored orange rather than red (Zellner et al., 1991).

Charles Spence (2020), in a review of "wine psychology," notes that there is a large amount of evidence that color influences the aroma, taste, and flavor of wine. He also notes that even wine experts can be fooled by deliberately miscoloring wine. This was demonstrated in a paper titled "Drinking Through Rosé-Colored Glasses," by Qian Wang and Spence (2019) in which wine experts were asked to rate the aroma and flavor of a white wine, a rosé wine, and "fake rosé" wine, which was the white wine dyed with food coloring so it matched the color of the real rosé wine. Magically, the food coloring caused the experts to describe the aroma and flavor of the fake rosé as being very similar to the real rosé and very different from the white wine. Most notably, the fake rosé and the real rosé received high ratings for "red fruit" aroma and taste, while the red fruit rating for the white wine was near zero.

Odors Can Influence Attention and Performance Participants sat in a cubicle, and were given the task of determining, as quickly as possible, whether a string of letters was a real word (like *bicycle*) or a non-word (like *poetsen*). Six of the real words were related to cleaning (like *hygiene*). When the smell of citrus, which is often associated with cleaning products, was infused into the cubicle, participants responded faster to the cleaning words, but the smell had no effect on the words that weren't related to cleaning (Holland et al., 2005). In another experiment, participants expected to perform better and actually did perform better on an analytical reasoning task when the testing room smelled like coffee, compared to when they took the test in an unscented environment (Madzharov et al., 2018). (Why do you think smelling coffee caused this effect? See page 415 for the answer.)

Results in both the "correspondences" and "influences" categories show that taste, smell, and flavor do not operate in isolation. They share correspondences with other senses, interact with them, affect them, and are affected by them. But why do these effects occur? One answer is "learning." Many associations are formed from everyday experiences. An obvious example is associating lemon flavor and yellow, strawberry and red. Also, odors of edible substances are likely to be associated with yellow, whereas odors that seem "inedible" are likely to be associated with blue, since blue is less likely to be associated with food. Paralleling the birdsong example at the beginning of this section, our experience tells us that a large dog is likely to have a lower pitched bark than a small dog.

Some correspondences can be explained by pleasure or emotions. Bright colors, often associated with happiness, are associated with pleasant odors. Similarly, pleasant odors are associated with the pleasant feelings from stroking soft fabrics.

Although learning from everyday experience and taking emotions into account can't explain all correspondences and influences, there is no question that much of perception is multimodal, and that it is accurate to describe the different senses as all part of a "community."

DEVELOPMENTAL DIMENSION Infant Chemical Sensitivity

Do newborn infants perceive odors and tastes? One way researchers have answered this question is to measure newborn facial expressions. **Figure 16.31** shows a newborn's response to the sweet taste of sucrose (left) and the bitter taste of quinine (right) (Rosenstein & Oster, 1988). It has also been shown that 3- to 7-day-old infants respond to banana extract or vanilla extract

Figure 16.31 Newborn facial expressions to the sweet taste of sucrose (left) and to the bitter taste of quinine (right), presented approximately 2 hours after birth and before the first feeding. (From Rosenstein & Oster, 1988)

Continued

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with sucking and facial expressions that are similar to smiles, and they respond to concentrated shrimp odor and an odor resembling rotten eggs with rejection or disgust (Steiner, 1974, 1979).

Research studying how newborns and young infants respond to salt indicates that there is a shift toward greater acceptance of salty solutions between birth and 4 to 8 months of age that continues into childhood (Beauchamp et al., 1994). One explanation for this shift is that it reflects the development of receptors sensitive to salt during infancy. But there is also evidence that infants' preferences are shaped by experience that occurs both before birth and during early infancy.

Figure 16.32 shows a number of ways that experience can shape the response to flavors, from pregnancy to weaning (Forestell, 2017). What the mother eats during pregnancy changes the flavor profile of the amniotic fluid, which affects the developing fetus, because by the last trimester, the taste and olfactory receptors are functioning and the fetus swallows between 500 and 1,000 ml of amniotic fluid a day (Forestell, 2017; Ross & Nijland, 1997). An experiment by Julie Mennella and coworkers (2001) provides evidence that the flavor of the amniotic fluid can influence an infant's preferences.

Mennella's experiment involved three groups of pregnant women, as shown in **Table 16.4**. Group 1 drank carrot juice during their final trimester of pregnancy and water during the first two months of lactation, when they were breast-feeding their infants. Group 2 drank water during pregnancy and carrot juice during the first two months of lactation, and Group 3 drank water during both periods. The infants' preference for carrot-flavored cereal versus plain cereal was tested four weeks after they had begun eating cereal but before they had experienced any food or juice containing a carrot flavor. The results, shown in the right column of Table 16.4, indicate that the infants who had experienced carrot flavor either in utero or in the mother's milk showed a preference for the carrot-flavored cereal (indicated by a score above 0.5), whereas the infants whose mothers had consumed only water showed no preference.

Table 16.4 Effect of What the Mother Consumes on Infant Preferences

GROUP	LAST TRIMESTER	DURING BREAST-FEEDING	INTAKE OF CARROT FLAVOR
1	Carrot juice	Water	0.62
2	Water	Carrot juice	0.57
3	Water	Water	0.51

Note: Intake score above 0.50 indicates preference for carrot-flavored cereal.

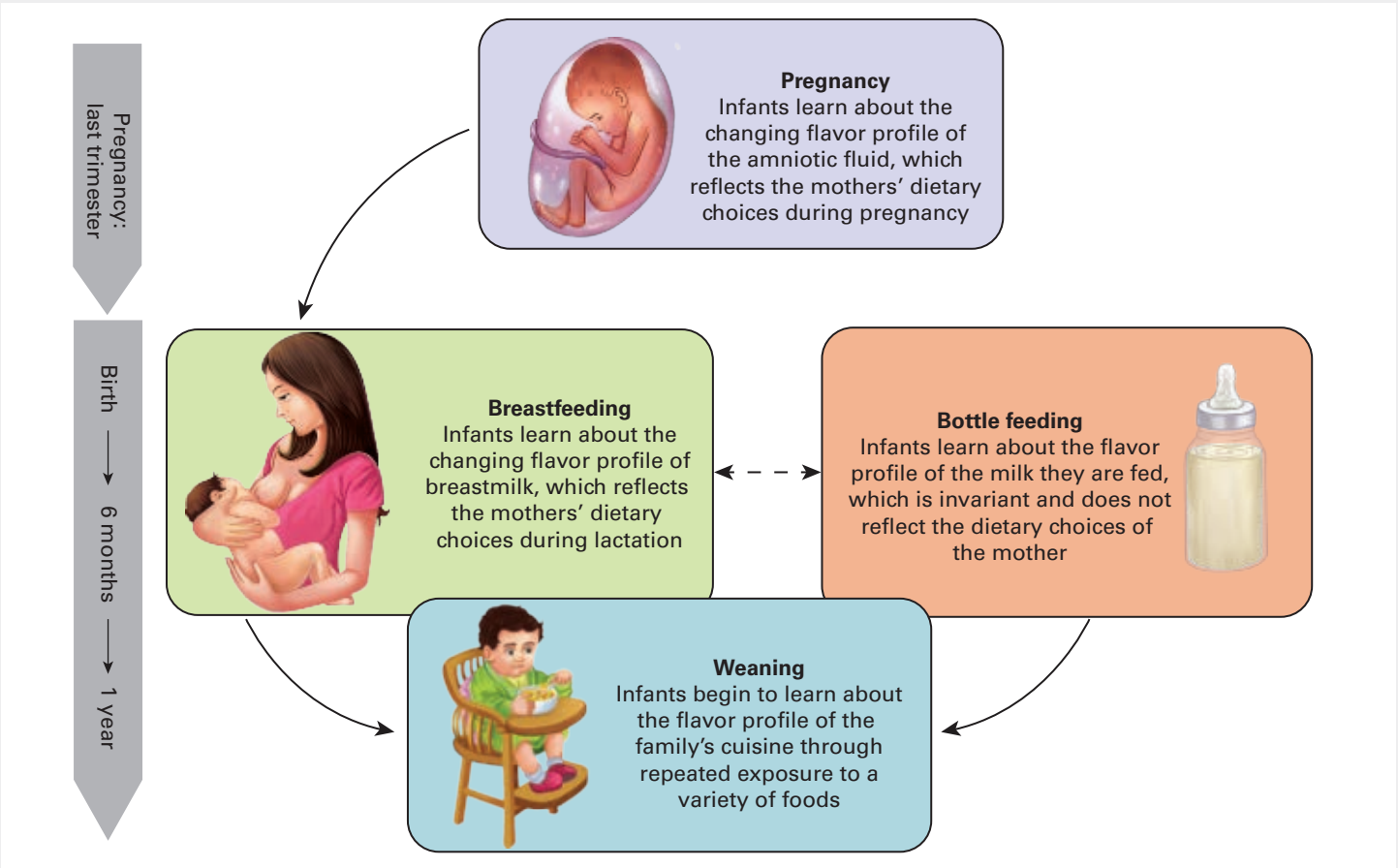
Pregnancy: last trimester
Birth
6 months
1 year
Pregnancy
Infants learn about the changing flavor profile of the amniotic fluid, which reflects the mothers' dietary choices during pregnancy
Breastfeeding
Infants learn about the changing flavor profile of breastmilk, which reflects the mothers' dietary choices during lactation
Bottle feeding
Infants learn about the flavor profile of the milk they are fed, which is invariant and does not reflect the dietary choices of the mother
Weaning
Infants begin to learn about the flavor profile of the family's cuisine through repeated exposure to a variety of foods

Figure 16.32 What infants learn during different stages of feeding. See text for explanation. (From Forestell, 2017)

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Returning to Figure 16.32, notice the contrast between breast-feeding and bottle feeding. The advantage of breast-feeding is that the taste of mother's milk is influenced by what she eats. So if a mother eats a lot of vegetables, the infant is drinking "vegetable flavored milk" and becomes familiar with that flavor. This translates into increased acceptance of vegetables when the child is older, which is a healthy food choice not always made by infants. Bottle feeding, in contrast, teaches infants about the flavor of whatever milk is in the formula, so the infant is not sharing the mothers' dietary choices.

Finally, when the child is weaned to solid food, its preferences are influenced first by what was experienced in the womb, then during nursing, and finally by exposure to the solid foods chosen by the child's family. Infants' responses to tastes, odors, and flavors are, therefore, determined both by innate factors, indicated by the fact that most newborns respond positively to sweet and negatively to bitter, and by experience, indicated by the way the mother's diet can influence the child's preferences. Thus, the first step toward insuring that young children develop good eating habits is for mothers to eat healthy foods, both when pregnant and while nursing.

TEST YOURSELF 16.3

1. What are the main structures in the olfactory system past the olfactory bulb?
2. How are odors represented in the piriform cortex? How does this representation differ from the representation in the olfactory bulb?
3. How has formation of the representation of odor objects in the cortex been described as being caused by experience? How is this similar to the process of forming memories?
4. What is the Proust effect? What are some properties of Proustian memories?
5. What is flavor perception? Describe how taste and olfaction meet in the mouth and nose and then later in the nervous system.
6. Describe the experiment that showed how expectations about a wine's taste can influence taste judgments and brain responding.
7. Describe the experiment that demonstrates sensory-specific satiety.
8. What does it mean to say that there is a "community" of senses?
9. Give examples of connections between chemical senses and (a) pitches and instruments, (b) colors, (c) texture, (d) attention and performance.
10. What is the evidence that newborns can detect different taste and smell qualities? Describe the carrot juice experiment and how it demonstrates that what a mother consumes can influence infant taste preferences.

THINK ABOUT IT

1. Consider the kinds of food that you avoid because you don't like the taste. Do these foods have anything in common that might enable you to explain these taste preferences in terms of the activity of specific types of taste receptors? (p. 396)
2. Can you think of situations in which you have encountered a smell that triggered memories about an event or place that you hadn't thought about in years? Do you think your experience was a "Proustian" memory? (p. 407)

Answer to question on page 413: One possible explanation for why coffee odor would cause higher expectations and better performance is that people often associate being in a coffee-scented environment, like a coffee shop, with the physiological arousal caused by drinking coffee.

KEY TERMS

Across-fiber patterns (p. 393)
Alzheimer's disease (p. 399)
Amiloride (p. 395)
Amygdala (p. 405)
Anosmia (p. 389)
Bimodal neuron (p. 409)
Calcium imaging (p. 402)
Chemotopic map (p. 403)
COVID-19 (p. 399)
Detection threshold (p. 398)
Flavor (p. 390)
Forced-choice method (p. 398)
Frontal operculum (p. 393)
Glomeruli (p. 403)
Insula (p. 393)

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Macrosmatic (p. 397)
Microsmatic (p. 397)
Mild cognitive impairment (p. 399)
Multimodal interactions (p. 411)
Nasal pharynx (p. 408)
Neurogenesis (p. 390)
Nucleus of the solitary tract (p. 392)
Odor map (p. 403)
Odor object (p. 401)
Odor-evoked autobiographical memory (p. 407)
Odotoptic map (p. 403)
Olfaction (p. 390)
Olfactory bulb (p. 401)
Olfactory mucosa (p. 401)
Olfactory receptor neurons (ORNs) (p. 401)
Olfactory receptors (p. 401)
Oral capture (p. 408)
Orbitofrontal cortex (p. 405)
Papillae (p. 391)
Piriform cortex (PC) (p. 405)
Primary olfactory area (p. 405)
Proust effect (p. 407)
Recognition profile (p. 403)
Retronasal route (p. 408)
Secondary olfactory area (p. 405)
Sensory-specific satiety (p. 410)
Sustentacular cell (p. 399)
Taste (p. 390)
Taste bud (p. 391)
Taste cell (p. 392)
Taste pore (p. 392)

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APPENDIX

A

The Difference Threshold

When Fechner published *Elements of Psychophysics*, he not only described his methods for measuring the absolute threshold but also described the work of Ernst Weber (1795–1878), a physiologist who, a few years before the publication of Fechner's book, measured another type of threshold, the **difference threshold**: the minimum *difference* that must exist *between* two stimuli before we can tell the difference between them. This just detectible difference is the difference threshold (also called DL from the German *Differenze Limen*, which is translated as "difference threshold").

Measuring instruments, such as an old-fashioned balance scale, can detect very small differences. For example, imagine that a scale is balanced when four 50-penny rolls are placed on each pan. When just one additional penny is placed on one side, the scale succeeds in detecting this very small difference between the two weights. The human sensory system is not as sensitive to weight differences as this type of scale, so a human comparing the weight of 201 pennies to 200 pennies would not be able to tell the difference. The difference threshold for weight is about 2 percent, which means that under ideal conditions, we would have to add 4 pennies to one side before the difference could be detected by the human.

The idea that the difference threshold is a *percentage* of the weights being compared was discovered by Weber, who proposed that the ratio of the DL to the standard is constant. This means that if we doubled the number of pennies to 400, the DL would also double, becoming 8. The ratio DL/Standard for lifting weights is 0.02, which is called the **Weber fraction**, and the fact that the Weber fraction remains the same as the standard is changed is called **Weber's law**. Modern investigators have found that Weber's law is true for most senses, as long as the stimulus intensity is not too close to the absolute threshold (Engen, 1972; Gescheider, 1976).

The Weber fraction remains relatively constant for a particular sense, but each type of sensory judgment has its own Weber fraction. For example, from **Table A.1** we can see that people can detect a 1 percent change in the intensity of an electric shock but that light intensity must be increased by 8 percent before they can detect a difference.

Table A.1 Weber Fractions for a Number of Different Sensory Dimensions

Electric shock	0.01
Lifted weight	0.02
Sound intensity	0.04
Light intensity	0.08
Taste (salty)	0.08

Source: Teghtsoonian (1971).

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APPENDIX

B

Magnitude Estimation and the Power Function

The procedure for a magnitude estimation experiment was described in Chapter 1 (p. 16). **Figure B.1** shows a graph that plots the results of a magnitude estimation experiment in which participants assigned numbers to indicate their perception of the brightness of lights. This graph, which presents the average magnitude estimates made by a number of participants, indicates that doubling the intensity does not necessarily double the perceived brightness. For example, when the intensity is 20, perceived brightness is 28. If we double the intensity to 40, perceived brightness does not double to 56, but instead increases only to 36. This result, in which the increase in perceived magnitude is smaller than the increase in stimulus intensity, is called **response compression**.

Figure B.1 also shows the results of magnitude estimation experiments for the experience caused by an electric shock presented to the finger and for the perception of length of a line. The electric shock curve bends up, indicating that doubling the strength of a shock more than doubles the perceived magnitude of the shock. Increasing the intensity from 20 to 40 increases perception of shock magnitude from 6 to 49. This is called **response expansion**. As intensity is increased, perceptual magnitude increases more than intensity. The curve for estimating line length is straight, with a slope of close to 1.0, meaning that the magnitude of the response almost exactly matches increases in the stimulus, so if the line length is doubled, an observer says it appears to be twice as long.

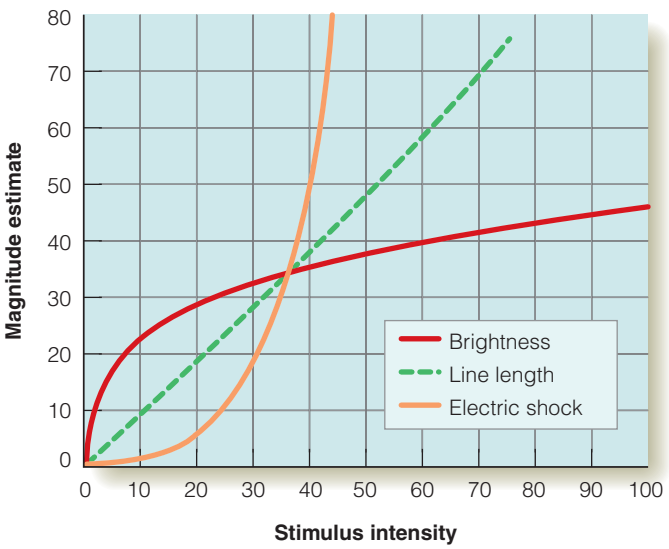

Figure B.1 The relationship between perceived magnitude and stimulus intensity for electric shock, line length, and brightness.
(Adapted from Stevens, 1962)

The beauty of the relationships derived from magnitude estimation is that the relationship between the intensity of a stimulus and our perception of its magnitude follows the same general equation for each sense. These functions, which are called **power functions**, are described by the equation $P = KS^n$. Perceived magnitude, P, equals a constant, K, times the stimulus intensity, S, raised to a power, n. This relationship is called **Stevens's power law**.

For example, if the exponent, n, is 2.0 and the constant, K, is 1.0, the perceived magnitude, P, for intensities 10 and 20 would be calculated as follows:

Intensity 10: $P = (1.0) \times (10)^2 = 100$

Intensity 20: $P = (1.0) \times (20)^2 = 400$

In this example, doubling the intensity results in a fourfold increase in perceived magnitude, an example of response expansion.

The exponent of the power function, n, tells us something important about the way perceived magnitude changes as intensity is increased. Exponents less than 1.0 are associated with response compression (as occurs for the brightness of a light), and exponents greater than 1.0 are associated with response expansion (as occurs for sensing shocks).

Response compression and expansion illustrate how the operation of each sense is adapted to how organisms function in their environment. Consider, for example, your experience of brightness. Imagine you are inside reading a book, when you turn to look out the window at a sidewalk bathed in intense sunlight. Your eyes may be receiving thousands of times more light from the sidewalk than from the page of your book, but because of response compression, the sidewalk does not appear thousands

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of times brighter than the page. It does appear brighter, but not so much that you are blinded by the sunlit sidewalk.[1]

[1]Another mechanism that keeps you from being blinded by high-intensity lights is the process of adaptation, which adjusts the eye's sensitivity in response to different light levels (see Chapter 3, page 46).

The opposite situation occurs for electric shock, which has an exponent of 3.5, so small increases in shock intensity cause large increases in pain. This rapid increase in pain associated with response expansion serves to warn us of impending danger, and we therefore tend to withdraw even from weak shocks.

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APPENDIX

C

The Signal Detection Approach

In Chapter 1 we saw that by randomly presenting stimuli of different intensities, we can use the method of constant stimuli to determine a person's threshold—the intensity to which the person reports "I see the light" or "I hear the tone" 50 percent of the time (p. 14). What determines this threshold intensity? Certainly, the physiological workings of the person's eye and visual system are important. But some researchers have pointed out that perhaps other characteristics of the person may also influence the determination of threshold intensity.

To illustrate this idea, let's consider a hypothetical experiment in which we use the method of constant stimuli to measure Lucy's and Cathy's thresholds for seeing a light. We pick five different light intensities, present them in random order, and ask Lucy and Cathy to say "yes" if they see the light and "no" if they don't see it. Lucy thinks about these instructions and decides that she wants to be sure she doesn't miss any presentations of the light. Because Lucy decides to say "yes" if there is even the slightest possibility that she sees the light, we could call her a liberal responder. Cathy, however, is a conservative responder. She wants to be totally sure that she sees the light before saying "yes" and so reports that she sees the light only if she is definitely sure she saw it.

The results of this hypothetical experiment are shown in **Figure C.1**. Lucy gives many more "yes" responses than Cathy does and therefore ends up with a lower threshold. But given what we know about Lucy and Cathy, should we conclude that Lucy's visual system is more sensitive to the lights than Cathy's? It could be that their actual sensitivity to the lights is exactly same, but Lucy's apparently lower threshold occurs because she is more willing than Cathy to report that she sees a light. A way to describe this difference between these two people is that each has a different **response criterion**. Lucy's response criterion is low (she says "yes" if there is the slightest chance a light is present), whereas Cathy's response criterion is high (she says "yes" only when she is sure that she sees the light).

What are the implications of the fact that people may have different response criteria? If we are interested in how one person responds to different stimuli (for example, measuring how a person's threshold varies for different colors of light), then we don't need to take response criterion into account because we are comparing responses within the same person. Response

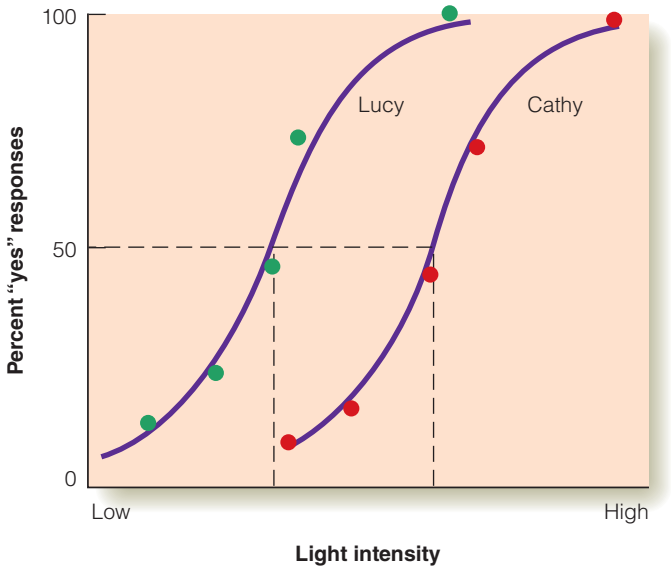

Figure C.1 Data from experiments in which the threshold for seeing a light is determined for Lucy (green points) and Cathy (red points) by means of the method of constant stimuli. These data indicate that Lucy's threshold is lower than Cathy's. But is Lucy really more sensitive to the light than Cathy, or does she just appear to be more sensitive because she is a more liberal responder?

criterion is also not very important if we are testing many people and averaging their responses. However, if we wish to compare two people's responses, their differing response criteria could influence the results. Luckily, an approach called the **signal detection approach** can be used to take differing response criteria into account. We will first describe a signal detection experiment and then describe the theory underlying the experiment.

A Signal Detection Experiment

Remember that in a psychophysical procedure such as the method of constant stimuli, at least five different stimulus intensities are presented and a stimulus is presented on

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every trial. In a signal detection experiment studying the detection of tones, we use only a single low-intensity tone that is difficult to hear, and we present this tone on some of the trials and present no tone at all on the rest of the trials.

The Basic Experiment

A signal detection experiment differs from a classical psychophysical experiment in two ways: (1) only one stimulus intensity is presented, and (2) on some of the trials, no stimulus is presented. Let's consider the results of such an experiment, using Lucy as our subject. We present the tone for 100 trials and no tone for 100 trials, mixing the tone and no-tone trials at random. Lucy's results are as follows.

When the tone is presented, Lucy

- Says "yes" on 90 trials. This correct response—saying "yes" when a stimulus is present—is called a **hit** in signal detection terminology.
- Says "no" on 10 trials. This incorrect response—saying "no" when a stimulus is present—is called a **miss**.

When no tone is presented, Lucy

- Says "yes" on 40 trials. This incorrect response—saying "yes" when there is no stimulus—is called a **false alarm**.
- Says "no" on 60 trials. This correct response—saying "no" when there is no stimulus—is called a **correct rejection**.

These results are not very surprising, given that we know Lucy has a low criterion and likes to say "yes" a lot. This gives her a high hit rate of 90 percent but also causes her to say "yes" on many trials when no tone is present, so her 90 percent hit rate is accompanied by a 40 percent false-alarm rate. If we do a similar experiment on Cathy, who has a higher criterion and therefore says "yes" much less often, we find that she has a lower hit rate (say, 60 percent) but also a lower false-alarm rate (say, 10 percent). Note that although Lucy and Cathy say "yes" on numerous trials on which no stimulus is presented, that result would not be predicted by classical threshold theory. Classical theory would say "no stimulus, no response," but that is clearly not the case here. By adding the following new wrinkle to our signal detection experiment, we can obtain another result that would not be predicted by classical threshold theory.

Payoffs

Without changing the tone's intensity at all, we can cause Lucy and Cathy to change their percentages of hits and false alarms. We do this by manipulating each person's motivation by means of **payoffs**. Let's look at how payoffs might influence Cathy's responding. Remember that Cathy is a conservative responder who is hesitant to say "yes." But being clever experimenters, we can make Cathy say "yes" more frequently by adding some financial inducements to the experiment. We tell Cathy that we are going to reward her for making correct responses and are going to penalize her for making incorrect responses by using the following payoffs.

Hit:	Win $100
Correct rejection:	Win $10
False alarm:	Lose $10
Miss:	Lose $10

What would you do if you were in Cathy's position? You realize that the way to make money is to say "yes" more. You can lose $10 if a "yes" response results in a false alarm, but this small loss is more than counterbalanced by the $100 you can win for a hit. Although you decide not to say "yes" on every trial—after all, you want to be honest with the experimenter about whether you heard the tone—you decide to stop being so conservative. You decide to change your criterion for saying "yes." The results of this experiment are interesting. Cathy becomes a more liberal responder and says "yes" a lot more, responding with 98 percent hits and 90 percent false alarms.

This result is plotted as data point L (for "liberal" response) in **Figure C.2**, a plot of the percentage of hits versus the percentage of false alarms. The solid curve going through point L is called a **receiver operating characteristic (ROC) curve**. We will see why the ROC curve is important in a moment, but first let's see how we determine the other points on the curve. Doing this is simple: all we have to do is to change the payoffs. We can make Cathy raise her criterion and therefore respond more conservatively by means of the following payoffs.

Hit:	Win $10
Correct rejection:	Win $100
False alarm:	Lose $10
Miss:	Lose $10

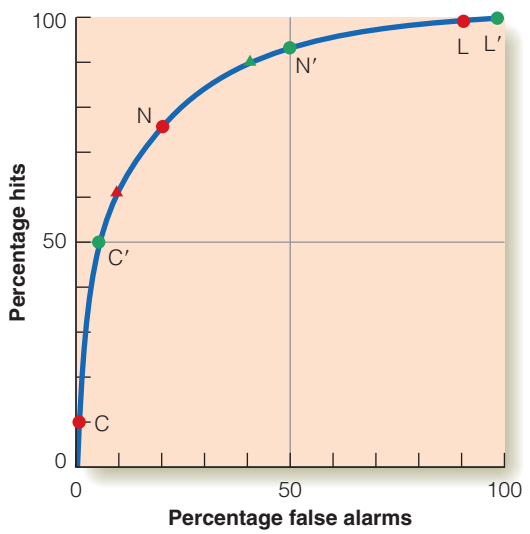

Figure C.2 A receiver operating characteristic (ROC) curve determined by testing Lucy (green data points) and Cathy (red data points) under three different criteria: liberal (L and L′), neutral (N and N′), and conservative (C and C′). The fact that Cathy's and Lucy's data points all fall on this curve means that they have the same sensitivity to the tone. The triangles indicate the results for Lucy and Cathy for an experiment that did not use payoffs.

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This schedule of payoffs offers a great inducement to respond conservatively because there is a big reward for saying "no" when no tone is presented. Cathy's criterion is therefore shifted to a much higher level, so Cathy now returns to her conservative ways and says "yes" only when she is quite certain that a tone is presented; otherwise she says "no." The result of this newfound conservatism is a hit rate of only 10 percent and a minuscule false-alarm rate of 1 percent, indicated by point C (for "conservative" response) on the ROC curve. We should note that although Cathy hits on only 10 percent of the trials in which a tone is presented, she scores a phenomenal 99 percent correct rejections on trials in which a tone is not presented. (If there are 100 trials in which no tone is presented, then correct rejections + false alarms = 100. Because there was 1 false alarm, there must be 99 correct rejections.)

Cathy, by this time, is rich and decides to put a down payment on the electric car she's been dreaming about. (So far she's won $8,980 in the first experiment and $9,090 in the second experiment, for a total of $18,070! To be sure you understand how the payoff system works, check this calculation yourself. Remember that the signal was presented on 100 trials and was not presented on 100 trials.) However, we point out that she may need a little extra cash to buy that new laptop computer she's been thinking about, so she agrees to stick around for one more experiment. We now use the following neutral schedule of payoffs.

Hit:	Win $10
Correct rejection:	Win $10
False alarm:	Lose $10
Miss:	Lose $10

With this schedule, we obtain point N (for "neutral") on the ROC curve: 75 percent hits and 20 percent false alarms. Cathy wins $1,100 more and becomes the proud owner of a new laptop computer and we are the proud owners of the world's most expensive ROC curve. (Do not, at this point, go to the psychology department in search of the nearest signal detection experiment. In real life, the payoffs are quite a bit less than in our hypothetical example.)

What Does the ROC Curve Tell Us?

Cathy's ROC curve shows that factors other than sensitivity to the stimulus determine a person's response. Remember that in all of our experiments the intensity of the tone has remained constant. Even though we changed only the person's criterion, we succeeded in drastically changing the person's responses.

Other than demonstrating that people will change how they respond to an unchanging stimulus, what does the ROC curve tell us? Remember, at the beginning of this discussion, we said that a signal detection experiment can tell us whether Cathy and Lucy are equally sensitive to the tone. The beauty of signal detection theory is that the person's sensitivity is indicated by the shape of the ROC curve, so if experiments on two people result in identical ROC curves, their sensitivities must be equal. (This conclusion is not obvious from our discussion so far. We will explain below why the shape of the ROC curve is related to the person's sensitivity.) If we repeat the above experiments on Lucy, we get the following results (data points L′, N′, and C′ in Figure C.2):

Liberal Payoff
Hits = 99 percent
False alarms = 95 percent

Neutral Payoff
Hits = 92 percent
False alarms = 50 percent

Conservative Payoff
Hits = 50 percent
False alarms = 6 percent

The data points for Lucy's results are shown by the green circles in Figure C.2. Note that although these points are different from Cathy's, they fall on the same ROC curve as do Cathy's. We have also plotted the data points for the first experiments we did on Lucy (open triangle) and Cathy (filled triangle) before we introduced payoffs. These points also fall on the ROC curve.

That Cathy's and Lucy's data both fall on the same ROC curve indicates their equal sensitivity to the tones. This confirms our suspicion that the method of constant stimuli misled us into thinking that Lucy is more sensitive, when the real reason for her apparently greater sensitivity is her lower criterion for saying "yes."

Before we leave our signal detection experiment, it is important to note that signal detection procedures can be used without the elaborate payoffs that we described for Cathy and Lucy. Much briefer procedures, which we will describe shortly, can be used to determine whether differences in the responses of different persons are due to differences in threshold or to differences in response criteria.

What does signal detection theory tell us about functions such as the spectral sensitivity curve (Figure 3.15, page 50) and the audibility curve (Figure 11.8, page 269), which are usually determined using one of the classical psychophysical methods? When the classical methods are used to determine these functions, it is usually assumed that the person's criterion remains constant throughout the experiment, so that the function measured is due not to changes in response criterion but to changes in the wavelength or some other physical property of the stimulus. This is a good assumption because changing the wavelength of the stimulus probably has little or no effect on factors such as motivation, which would shift the person's criterion. Furthermore, experiments such as the one for determining the spectral sensitivity curve usually use highly experienced people who are trained to give stable results. Thus, even though the idea of an "absolute threshold" may not be strictly correct, classical psychophysical experiments run under well-controlled conditions have remained an important tool for measuring the relationship between stimuli and perception.

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Signal Detection Theory

We will now discuss the theoretical basis for the signal detection experiments we have just described. Our purpose is to explain the theoretical bases underlying two ideas: (1) the percentage of hits and false alarms depends on a person's criterion, and (2) a person's sensitivity to a stimulus is indicated by the shape of the person's ROC curve. We will begin by describing two key concepts of signal detection theory (SDT): **signal** and **noise**. (See Swets, 1964.)

Signal and Noise

The **signal** is the stimulus presented to the person. Thus, in the signal detection experiment we just described, the signal is the tone. The **noise** is all the other stimuli in the environment, and because the signal is usually very faint, noise can sometimes be mistaken for the signal. Seeing what appears to be a flicker of light in a completely dark room is an example of visual noise. Seeing light where there is none is what we have been calling a false alarm, according to signal detection theory. False alarms are caused by the noise. In the experiment we just described, hearing a tone on a trial in which no tone was presented is an example of auditory noise.

Let's now consider a typical signal detection experiment, in which a signal is presented on some trials and no signal is presented on the other trials. Signal detection theory describes this procedure not in terms of presenting a signal or no signal, but in terms of presenting signal plus noise (S + N) or noise (N). That is, the noise is always present, and on some trials, we add a signal. Either condition can result in the perceptual effect of hearing a tone. A false alarm occurs when the person says "yes" on a noise trial, and a hit occurs when the person says "yes" on a signal-plus-noise trial. Now that we have defined signal and noise, we introduce the idea of probability distributions for noise and signal plus noise.

Probability Distributions

Figure C.3 shows two probability distributions. The one on the left represents the probability that a given perceptual effect will be caused by noise (N), and the one on the right represents the probability that a given perceptual effect will be caused by signal plus noise (S + N). The key to understanding these distributions is to realize that the value labeled "Perceptual effect (loudness)" on the horizontal axis is what the person experiences on each trial. Thus, in an experiment in which the person is asked to indicate whether a tone is present, the perceptual effect is the perceived loudness of the tone. Remember that in an SDT experiment the tone always has the same *intensity*. The *loudness* of the tone, however, can vary from trial to trial. The person perceives different loudnesses on different trials, because of either trial-to-trial changes in attention or changes in the state of the person's auditory system.

The probability distributions tell us what the chances are that a given loudness of tone is due to (N) or to (S + N). For example, let's assume that a person hears a tone with a loudness of 10 on one of the trials of a signal detection experiment. By extending a vertical dashed line up from 10 on the "Perceptual effect" axis in Figure C.3, we see that the probability that a loudness of 10 is due to (S + N) is extremely low, because the distribution for (S + N) is essentially zero at this loudness. There is, however, a fairly high probability that a loudness of 10 is due to (N), because the (N) distribution is fairly high at this point.

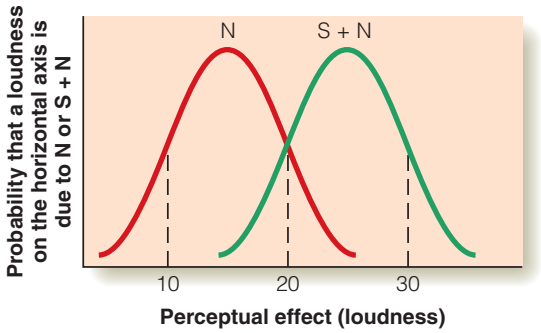

Figure C.3 Probability distributions for noise alone (N, red curve), and for signal plus noise (S + N, green curve). The probability that any given perceptual effect is caused by the noise (no signal is presented) or by the signal plus noise (signal is presented) can be determined by finding the value of the perceptual effect on the horizontal axis and extending a vertical line up from that value. The place where that line intersects the (N) and (S + N) distributions indicates the probability that the perceptual effect was caused by (N) or by (S + N).

Let's now assume that, on another trial, the person perceives a loudness of 20. The probability distributions indicate that when the tone's loudness is 20, it is equally probable that this loudness is due to (N) or to (S + N). We can also see from Figure C.3 that a tone with a perceived loudness of 30 would have a high probability of being caused by (S + N) and only a small probability of being caused by (N).

Now that we understand the curves of Figure C.3, we can appreciate the problem confronting the person. On each trial, she has to decide whether no tone (N) was present or whether a tone (S + N) was present. However, the overlap in the probability distributions for (N) and (S + N) means that for some perceptual effects this judgment will be difficult. As we saw before, it is equally probable that a tone with a loudness of 20 is due to (N) or to (S + N). So, on a trial in which the person hears a tone with a loudness of 20, how does she decide whether the signal was presented? According to signal detection theory, the person's decision depends on the location of her criterion.

The Criterion

We can see how the criterion affects the person's response by looking at **Figure C.4**. In this figure, we have labeled three different criteria: liberal (L), neutral (N), and conservative (C). Remember that we can cause people to adopt these different criteria by means of different payoffs. According to signal detection theory, once the person adopts a criterion, he or she

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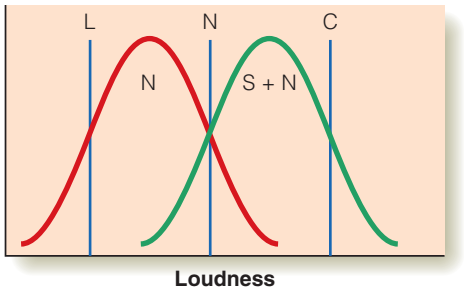

Figure C.4 The same probability distributions from Figure C.3, showing three criteria: liberal (L), neutral (N), and conservative (C). When a person adopts a criterion, he or she uses the following decision rule: Respond "yes" ("I detect the stimulus") when the perceptual effect is greater than the criterion, and respond "no" ("I do not detect the stimulus") when the perceptual effect is less than the criterion.

uses the following rule to decide how to respond on a given trial: If the perceptual effect is greater than (to the right of) the criterion, say "Yes, the tone was present"; if the perceptual effect is less than (to the left of) the criterion, say "No, the tone was not present." Let's consider how different criteria influence the person's hits and false alarms.

To determine how the criterion affects the person's hits and false alarms, we will consider what happens when we present (N) and when we present (S + N) under three different criteria.

Liberal Criterion

1. Present (N): Because most of the probability distribution for (N) falls to the right of the criterion, the chances are good that presenting (N) will result in a loudness to the right of the criterion. This means that the probability of saying "yes" when (N) is presented is high; therefore, the probability of a false alarm is high.
2. Present (S + N): Because the entire probability distribution for (S + N) falls to the right of the criterion, the chances are excellent that presenting (S + N) will result in a loudness to the right of the criterion. Thus, the probability of saying "yes" when the signal is presented is high; therefore, the probability of a hit is high. Because criterion L results in high false alarms and high hits, adopting that criterion will result in point L on the ROC curve in **Figure C.5**.

Neutral Criterion

1. Present (N): The person will answer "yes" only rarely when (N) is presented because only a small portion of the (N) distribution falls to the right of the criterion. The false-alarm rate, therefore, will be fairly low.
2. Present (S + N): The person will answer "yes" frequently when (S + N) is presented because most of the (S + N) distribution falls to the right of the criterion. The hit rate, therefore, will be fairly high (but not as high as for the L criterion). Criterion N results in point N on the ROC curve in Figure C.5.

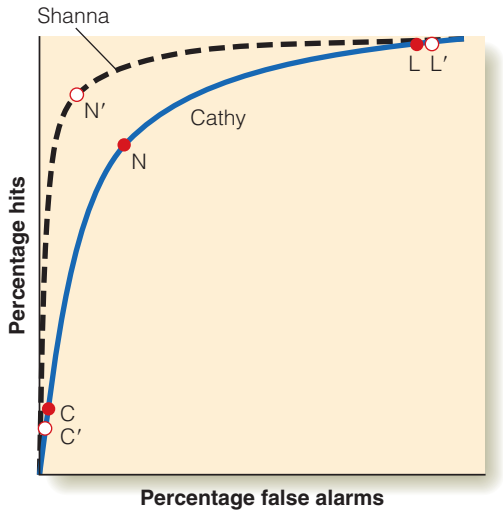

Figure C.5 ROC curves for Cathy (solid curve) and Shanna (dashed curve) determined using liberal (L, L′), neutral (N, N′), and conservative (C, C′) criteria.

Conservative Criterion

1. Present (N): False alarms will be very low because none of the (N) curve falls to the right of the criterion.
2. Present (S + N): Hits will also be low because only a small portion of the (S + N) curve falls to the right of the criterion. Criterion C results in point C on the ROC curve in Figure C.5.

You can see that applying different criteria to the probability distributions generates the solid ROC curve in Figure C.5. But why are these probability distributions necessary? After all, when we described the experiment with Cathy and Lucy, we determined the ROC curve simply by plotting the results of the experiment. The reason the (N) and (S + N) distributions are important is that, according to signal detection theory, the person's sensitivity to a stimulus is indicated by the distance (d′) between the peaks of the (N) and (S + N) distributions, and this distance affects the shape of the ROC curve. We will now consider how the person's sensitivity to a stimulus affects the shape of the ROC curve.

The Effect of Sensitivity on the ROC Curve

We can understand how the person's sensitivity to a stimulus affects the shape of the ROC curve by considering what the probability distributions would look like for Shanna, a person with supersensitive hearing. Shanna's hearing is so good that a tone barely audible to Cathy sounds very loud to Shanna. If presenting (S + N) causes Shanna to hear a loud tone, this means that her (S + N) distribution should be far to the right, as shown in **Figure C.6**. In signal detection terms, we would say that Shanna's high sensitivity is indicated by the large separation (d′) between the (N) and the (S + N) probability distributions. To see how this greater separation between the probability distributions will affect her ROC curve, let's see how she would respond when adopting liberal, neutral, and conservative criteria.

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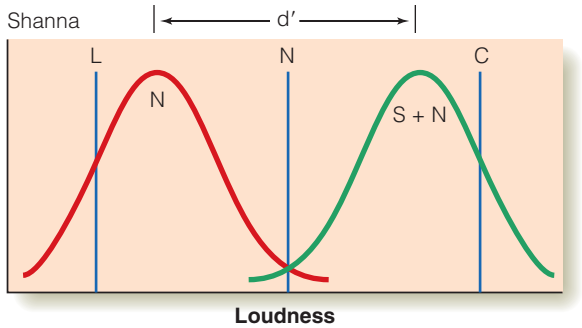

Figure C.6 Probability distributions for Shanna, a person who is extremely sensitive to the signal. The noise distribution (red) remains the same, but the (S + N) distribution (green) is shifted to the right compared to the curves in Figure C.4. Liberal (L), neutral (N), and conservative (C) criteria are shown.

Liberal Criterion

1. Present (N): high false alarms.
2. Present (S + N): high hits.

The liberal criterion, therefore, results in point L′ on the ROC curve of Figure C.5.

Neutral Criterion

1. Present (N): low false alarms. It is important to note that Shanna's false alarms for the neutral criterion will be lower than Cathy's false alarms for the neutral criterion because only a very small portion of Shanna's (N) distribution falls to the right of the criterion, whereas more of Cathy's (N) distribution falls to the right of the neutral criterion (Figure C.4).
2. Present (S + N): high hits.

In this case, Shanna's hits will be higher than Cathy's because almost all of Shanna's (S + N) distribution falls to the right of the neutral criterion, whereas less of Cathy's does (Figure C.4). The neutral criterion, therefore, results in point N′ on the ROC curve in Figure C.5.

Conservative Criterion

1. Present (N): low false alarms.
2. Present (S + N): low hits.

The conservative criterion, therefore, results in point C′ on the ROC curve.

The difference between the two ROC curves in Figure C.5 is obvious because Shanna's curve is more "bowed." But before you conclude that the difference between these two ROC curves has anything to do with where we positioned Shanna's L, N, and C criteria, see whether you can get an ROC curve like Shanna's from the two probability distributions of Figure C.4. You will find that, no matter where you position the criteria, there is no way that you can get a point like point N′ (with very high hits and very low false alarms) from the curves of Figure C.4. In order to achieve very high hits and very low false alarms, the two probability distributions must be spaced far apart, as in Figure C.6.

Thus, increasing the distance (d′) between the (N) and the (S + N) probability distributions changes the shape of the ROC curve. When the person's sensitivity (d′) is high, the ROC curve is more bowed. In practice, d′ can be determined by comparing the experimentally determined ROC curve to standard ROC curves (see Gescheider, 1976), or d′ can be calculated from the proportions of hits and false alarms that occur in an experiment by means of a mathematical procedure we will not discuss here. This mathematical procedure for calculating d′ enables us to determine a person's sensitivity by determining only one data point on an ROC curve, thus using the signal detection procedure without running a large number of trials.

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Glossary

The number in parentheses at the end of each entry indicates the chapter in which the term is first used.

#TheDress The online address for a picture of a dress that is seen as alternating blue and black stripes by some people and as alternating white and gold stripes by others. (9)

Aberrations Imperfections on the eye's cornea and lens that distort light on its way to the retina. (9)

Ablation Removal of an area of the brain. This is usually done in experiments on animals to determine the function of a particular area. Also called lesioning. (4)

Absolute disparity *See* **Angle of disparity**. (10)

Absolute threshold The smallest stimulus level that can just be detected. (1)

Absorption spectrum A plot of the amount of light absorbed by a visual pigment versus the wavelength of light. (3)

Accommodation In vision, bringing objects located at different distances into focus by changing the shape of the lens. (3)

Accretion A cue that provides information about the relative depth of two surfaces. Occurs when the farther object is uncovered by the nearer object due to sideways movement of an observer relative to the objects. *See also* **Deletion**. (10)

Achromatic color Color without hue. White, black, and all the grays between these two extremes are achromatic colors. (9)

Acoustic shadow The shadow created by the head that decreases the level of high-frequency sounds on the opposite side of the head. The acoustic shadow is the basis of the localization cue of interaural level difference. (12)

Acoustic signal The pattern of frequencies and intensities of the sound stimulus. (14)

Acoustic stimulus *See* **Acoustic signal**. (14)

Across-fiber patterns The pattern of nerve firing that a stimulus causes across a number of neurons. Also referred to as distributed coding. (16)

Action Motor activities in response to a stimulus. (1)

Action affordance A response to an object that involves both its affordance (what it is for) and the action associated with it. (7)

***Action* pathway** *See* **Dorsal pathway**. (4)

Action potential Rapid increase in positive charge in a nerve fiber that travels down the fiber. Also called the nerve impulse. (2)

Action-specific perception hypothesis Hypothesis that people perceive their environment in terms of their ability to act on it. (7)

Active touch Touch in which the observer plays an active role in touching and exploring an object, usually with his or her hands. (15)

Adaptive optical imaging A technique that makes it possible to look into a person's eye and take pictures of the receptor array in the retina. (9)

Additive color mixture *See* **Color mixture, additive**. (9)

Adjustment, method of A psychophysical method in which the experimenter or the observer adjusts the stimulus intensity in a continuous manner until the observer detects the stimulus. (1)

Adult-directed speech Speech that is directed toward an adult. (14)

Affective (emotional) component of pain The emotional experience associated with pain—for example, pain described as *torturing*, *annoying*, *frightful*, or *sickening*. *See also* **Sensory component of pain**. (15)

Affective function of touch The eliciting of emotions by touch. (15)

Affordance The information specified by a stimulus pattern that indicates how the stimulus can be used. An example of an affordance would be seeing a chair as something to sit on or a flight of stairs as something to climb. (7)

Agnosia *See* **Visual form agnosia**. (1)

Akinetopsia A condition in which damage to an area of the cortex involved in motion perception causes blindness to motion. (8)

Alzheimer's disease Serious loss of memory and other cognitive functions that is often preceded by mild cognitive impairment (MCI). (16)

Amacrine cell A neuron that transmits signals laterally in the retina. Amacrine cells synapse with bipolar cells and ganglion cells. (3)

Ames room A distorted room, first built by Adelbert Ames, that creates an erroneous perception of the sizes of people in the room. The room is constructed so that two people at the far wall of the room appear to stand at the same distance from an observer. In actuality, one of the people is much farther away than the other. (10)

Amiloride A substance that blocks the flow of sodium into taste receptors. (16)

Amplitude In the case of a repeating sound wave, such as the sine wave of a pure tone, amplitude represents the pressure difference between atmospheric pressure and the maximum pressure of the wave. (11)

Amplitude modulation Adjusting the level (or intensity) of a sound stimulus so it fluctuates up and down. (11)

Amplitude-modulated noise A noise sound stimulus that is amplitude modulated. (11)

Amygdala A subcortical structure that is involved in emotional responding and in processing olfactory signals. (16)

Angle of disparity The visual angle between the images of an object on the two retinas. When images of an object fall on corresponding points, the angle of disparity is zero. When images fall on noncorresponding points, the angle of disparity indicates the degree of noncorrespondence. (10)

Angular size contrast theory An explanation of the moon illusion that states that the perceived size of the moon is determined by the sizes of the objects that surround it. According to this idea, the moon appears small when it is surrounded by large objects, such as the expanse of the sky when the moon is overhead. (10)

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Anomalous trichromatism A type of color deficiency in which a person needs to mix a minimum of three wavelengths to match any other wavelength in the spectrum but mixes these wavelengths in different proportions than a trichromat. (9)

Anosmia Loss of the ability to smell due to injury or infection. (16)

Anterior belt area The front of the posterior belt in the temporal lobe, which is involved in perceiving sound. (12)

Aperiodic sound Sound waves that do not repeat. *See* **Periodic sound**. (11)

Aperture problem Occurs when only a portion of a moving stimulus can be seen, as when the stimulus is viewed through a narrow aperture or through the "field of view" of a neurons' receptive field. This can result in misleading information about the direction in which the stimulus is moving. (8)

Apex (of the cochlea) The end of the cochlea farthest from the middle ear. (11)

Aphasia Difficulties in speaking or understanding speech due to brain damage. (14)

Apparent distance theory An explanation of the moon illusion that is based on the idea that the horizon moon, which is viewed across the filled space of the terrain, should appear farther away than the zenith moon, which is viewed through the empty space of the sky. This theory states that because the horizon and zenith moons have the same visual angle but are perceived to be at different distances, the farther appearing horizon moon should appear larger. (10)

Apparent motion *See* **Apparent movement**. (8)

Apparent movement An illusion of movement that occurs when two objects separated in space are presented rapidly, one after another, separated by a brief time interval. (5)

Arch trajectory The rise and then fall in pitch commonly found in music. (13)

Architectural acoustics The study of how sounds are reflected in rooms. An important concern of architectural acoustics is how these reflected sounds change the quality of the sounds we hear. (12)

Area V1 The visual receiving area of the brain, called area V1 to indicate that it is the first visual area in the cortex. Also called the striate cortex. (4)

Articulator Structure involved in speech production, such as the tongue, lips, teeth, jaw, and soft palate. (14)

Atmospheric perspective A depth cue. Objects that are farther away look more blurred and bluer than objects that are closer because we look through more air and particles to see them. (10)

Attack The buildup of sound energy that occurs at the beginning of a tone. (11)

Attention The process of focusing on some objects while ignoring others. Attention can enhance the processing of the attended object. (6)

Attentional capture Occurs when stimulus salience causes an involuntary shift of attention. For example, attention can be captured by movement. (6)

Audibility curve A curve that indicates the sound pressure level (SPL) at threshold for frequencies across the audible spectrum. (11)

Audiogram Plot of hearing loss versus frequency. (11)

Audiovisual mirror neuron Neuron that responds to actions that produce sounds. These neurons respond when a monkey performs a hand action *and* when it hears the sound associated with this action. *See also* **Mirror neuron**. (7)

Audiovisual speech perception A perception of speech that is affected by both auditory and visual stimulation, as when a person sees a video of someone making the lip movements for /fa/ while hearing the sound /ba/ and perceives /fa/. Also called the McGurk effect. (14)

Auditory canal The canal through which air vibrations travel from the environment to the tympanic membrane. (11)

Auditory localization The perception of the location of a sound source. (12)

Auditory response area The psychophysically measured area that defines the frequencies and sound pressure levels over which hearing functions. This area extends between the audibility curve and the curve for the threshold of feeling. (11)

Auditory scene The sound environment, which includes the locations and qualities of individual sound sources. (12)

Auditory scene analysis The process by which the sound stimuli produced by different sources in an auditory scene become perceptually organized into sounds at different locations and into separated streams of sound. (12)

Auditory space Perception of where sounds are located in space. Auditory space extends around a listener's head in all directions, existing wherever there is a sound. (12)

Auditory stream segregation The effect that occurs when a series of sounds that differ in pitch or timbre are played so that the tones become perceptually separated into simultaneously occurring independent streams of sound. (12)

Automatic speech recognition (ASR) Using computers to recognize speech. (14)

Axial myopia Myopia (nearsightedness) in which the eyeball is too long. *See also* **Refractive myopia**. (3)

Axon The part of the neuron that conducts nerve impulses over distances. Also called the nerve fiber. (2)

Azimuth In hearing, specifies locations that vary from left to right relative to the listener. (12)

Base (of the cochlea) The end of the cochlea nearest the middle ear. (11)

Basilar membrane A membrane that stretches the length of the cochlea and controls the vibration of the cochlear partition. (11)

Bayesian inference A statistical approach to perception in which perception is determined by taking probabilities into account. These probabilities are based on past experiences in perceiving properties of objects and scenes. (5)

Beat In music, equally spaced intervals of time, which occurs even if there are no notes. When you tap your feet to music, you are tapping on the beat. (13)

Bimodal neuron A neuron that responds to stimuli associated with more than one sense. (16)

Binaural cue Sound localization cue that involves both ears. Interaural time difference and interaural level difference are the primary binaural cues. (12)

Binding The process by which features such as color, form, motion, and location are combined to create our perception of a coherent object. Binding can also occur across senses, as when sound and vision are associated with the same object. (6)

Binocular depth cell A neuron in the visual cortex that responds best to stimuli that fall on points separated by a specific degree of disparity on the two retinas. Also called a disparity-selective cell. (10)

Binocular disparity Occurs when the retinal images of an object fall on disparate points on the two retinas. (10)

Binocular rivalry A situation in which one image is presented to the left eye, a different image is presented to the right eye, and perception alternates back and forth between the two images. (5)

Binocularly fixate Directing the two foveas to exactly the same spot. (10)

Biological motion Motion produced by biological organisms. Most of the experiments on biological motion have used walking humans with lights attached to their joints and limbs as stimuli. *See also* **Point-light walker**. (8)

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Bipolar cell A retinal neuron that receives inputs from the visual receptors and sends signals to the retinal ganglion cells. (3)

Blind spot The small area where the optic nerve leaves the back of the eye. There are no visual receptors in this area, so small images falling directly on the blind spot cannot be seen. (3)

Border ownership When two areas share a border, as occurs in figure–ground displays, the border is usually perceived as belonging to the figure. (5)

Bottom-up processing Processing that is based on the information on the receptors. Also called data-based processing. (1)

Brain imaging Procedures that make it possible to visualize areas of the human brain that are activated by different types of stimuli, tasks, or behaviors. The most common technique used in perception research is functional magnetic resonance imaging (fMRI). (2)

Broca's aphasia Language problems including labored and stilted speech and short sentences, caused by damage to Broca's area in the frontal lobe. (13)

Broca's area An area in the frontal lobe that is important for language perception and production. One effect of damage is difficulty in speaking. (2)

Calcium imaging A method of measuring receptor activity by using fluorescence to measure the concentration of calcium inside the receptor. This technique has been used to measure the activation of olfactory receptor neurons. (16)

Categorical perception In speech perception, perceiving one sound at short voice onset times and another sound at longer voice onset times. The listener perceives only two categories across the whole range of voice onset times. (14)

Categorize Placing objects into categories, such as "tree," "bird," "car." (1)

Cell body The part of a neuron that contains the neuron's metabolic machinery and that receives stimulation from other neurons. (2)

Center-surround antagonism The competition between the center and surround regions of a center-surround receptive field, caused by the fact that one is excitatory and the other is inhibitory. Stimulating center and surround areas simultaneously decreases responding of the neuron, compared to stimulating the excitatory area alone. (3)

Center-surround receptive field A receptive field that has a center-surround organization. (3)

Cerebral achromatopsia A loss of color vision caused by damage to the cortex. (9)

Cerebral cortex The 2-mm-thick layer that covers the surface of the brain and contains the machinery for creating perception, as well as for other functions, such as language, memory, and thinking. (1)

Change blindness Difficulty in detecting differences between two visual stimuli that are presented one after another, often with a short blank stimulus interposed between them. Also occurs when part of a stimulus is changed very slowly. (6)

Characteristic frequency The frequency at which a neuron in the auditory system has its lowest threshold. (11)

Chemotopic map The pattern of activation in the olfactory system in which chemicals with different properties create a "map" of activation based on these properties. For example, there is evidence that chemicals are mapped in the olfactory bulb based on carbon-chain length. Also called odor map. (16)

Chevreul illusion Occurs when areas of different lightness are positioned adjacent to one another to create a border. The illusion is the perception of a light band on the light side of the border and a dark band on the dark side of the border, even though these bands do not exist in the intensity distribution. (3)

Chromatic adaptation Exposure to light in a specific part of the visible spectrum. This adaptation can cause a decrease in sensitivity to light from the area of the spectrum that was presented during adaptation. (9)

Chromatic color Color with hue, such as blue, yellow, red, or green. (9)

Classical psychophysical methods The methods of limits, adjustment, and constant stimuli, described by Fechner, that are used for measuring thresholds. (1)

Cloze probability task Task in which a listener is presented with a melody, which suddenly stops. The listener's task is to sing the note they think comes next. This task is also used in the study of language, in which case part of a sentence is presented and the listener predicts the word that will come next. (13)

Coarticulation The overlapping articulation that occurs when different phonemes follow one another in speech. Because of these effects, the same phoneme can be articulated differently depending on the context in which it appears. For example, articulation of the /b/ in *boot* is different from articulation of the /b/ in *boat.* (14)

Cochlea The snail-shaped, liquid-filled structure that contains the structures of the inner ear, the most important of which are the basilar membrane, the tectorial membrane, and the hair cells. (11)

Cochlear amplifier Expansion and contraction of the outer hair cells in response to sound sharpens the movement of the basilar membrane to specific frequencies. This amplifying effect plays an important role in determining the frequency selectivity of auditory nerve fibers. (11)

Cochlear implant A device in which electrodes are inserted into the cochlea to create hearing by electrically stimulating the auditory nerve fibers. This device is used to restore hearing in people who have lost their hearing because of damaged hair cells. (14)

Cochlear nucleus The nucleus where nerve fibers from the cochlea first synapse. (11)

Cochlear partition A partition in the cochlea, extending almost its full length, that separates the scala tympani and the scala vestibuli. The organ of Corti, which contains the hair cells, is part of the cochlear partition. (11)

Cocktail party effect The ability to focus on one stimulus while filtering out other stimuli, so called because at noisy parties people are able to focus on what one person is saying even though there are many conversations happening at the same time. (6)

Cognitive map A mental map of the spatial layout of an area of the environment. (7)

Cognitivist approach (to musical emotion) Approach to describing the emotional response to music which proposes that listeners can perceive the emotional meaning of a piece of music, but that they don't actually feel the emotions. (13)

Coherence In research on movement perception in which arrays of moving dots are used as stimuli, the degree of correlation between the direction of the moving dots. Zero percent coherence means all of the dots are moving independently; 100 percent coherence means all of the dots are moving in the same direction. (8)

Coincidence detectors Neurons in the Jeffress neural coincidence model, which was proposed to explain how neural firing can provide information regarding the location of a sound source. A neural coincidence detector fires when signals from the left and right ears reach the neuron simultaneously. Different neural coincidence detectors fire to different values of interaural time difference. *See also* **Jeffress model**. (12)

Color blindness A condition in which a person perceives no chromatic color. This can be caused by absent or malfunctioning cone receptors or by cortical damage. (9)

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Color circle Perceptually similar colors located next to each other and arranged in a circle. (9)

Color constancy The effect in which the perception of an object's hue remains constant even when the wavelength distribution of the illumination is changed. *Partial color constancy* occurs when our perception of hue changes a little when the illumination changes, though not as much as we might expect from the change in the wavelengths of light reaching the eye. (9)

Color deficiency Condition (sometimes incorrectly called color blindness) in which people see fewer colors than people with normal color vision and need to mix fewer wavelengths to match any other wavelength in the spectrum. (9)

Color mixture, additive The creation of colors that occurs when lights of different colors are superimposed. (9)

Color mixture, subtractive The creation of colors that occurs when paints of different colors are mixed together. (9)

Color matching A procedure in which observers are asked to match the color in one field by mixing two or more lights in another field. (9)

Color solid A solid in which colors are arranged in an orderly way based on their hue, saturation, and value. (9)

Common fate, principle of A Gestalt principle of perceptual organization that states that things that are moving in the same direction appear to be grouped together. (5)

Common region, principle of A modern Gestalt principle that states that elements that are within the same region of space appear to be grouped together. (5)

Comparator A structure hypothesized by the corollary discharge theory of movement perception. The corollary discharge signal and the sensory movement signal meet at the comparator to determine whether movement will be perceived. (6)

Complex cell A neuron in the visual cortex that responds best to moving bars with a particular orientation. (4)

Cone of confusion A surface in the shape of a cone that extends out from the ear. Sounds originating from different locations on this surface all have the same interaural level difference and interaural time difference, so location information provided by these cues is ambiguous. (12)

Cone mosaic Arrangement of short-, medium-, and long-wavelength cones in a particular area of the retina. (9)

Cone spectral sensitivity curve A plot of visual sensitivity versus wavelength for cone vision. Often measured by presenting a small spot of light to the fovea, which contains only cones. Can also be measured when the eye is light adapted, so cones are the most sensitive receptors. (3)

Cones Cone-shaped receptors in the retina that are primarily responsible for vision in high levels of illumination and for color vision and detail vision. (3)

Conflicting cues theory A theory of visual illusions proposed by R. H. Day, which states that our perception of line length depends on an integration of the actual line length and the overall figure length. (10)

Congenital amusia A condition in which a person doesn't recognize tones as tones and therefore does not experience sequences of tones as music. (13)

Conjunction search A visual search task in which it is necessary to search for a combination (or conjunction) of two or more features on the same stimulus to find the target. An example of a conjunction search would be looking for a horizontal green line among vertical green lines and horizontal red lines. (6)

Consonance The positive sound quality created when two or more pitches are played together. (13)

Constant stimuli, method of A psychophysical method in which a number of stimuli with different intensities are presented repeatedly in a random order. (1)

Contextual modulation Change in response to a stimulus presented within a neuron's receptive field caused by stimulation outside of the receptive field. (4)

Continuity error Mismatch, usually involving spatial position or objects, that occurs from one film shot to another. (6)

Contralateral Side of the body opposite to the side on which a particular condition occurs. (4)

Contrast threshold The intensity difference between two areas that can just barely be seen. This is often measured using gratings with alternating light and dark bars. (4)

Convergence (depth cue) *See* **Perspective convergence**. (10)

Convergence (neural) When many neurons synapse onto a single neuron. (3)

Cornea The transparent focusing element of the eye that is the first structure through which light passes as it enters the eye. The cornea is the eye's major focusing element. (3)

Corollary discharge signal (CDS) A copy of the motor signal that is sent to the eye muscles to cause movement of the eye. The copy is sent to the hypothetical comparator of corollary discharge theory. (6)

Corollary discharge theory The theory that explains motion perception as being determined both by movement of the image on the retina and by signals that indicate movement of the eyes. *See also* **Corollary discharge signal**. (6)

Correct rejection In a signal detection experiment, saying "No, I don't detect a stimulus" on a trial in which the stimulus is not presented (a correct response). (Appendix C)

Correspondence problem The problem faced by the visual system, which must determine which parts of the images in the left and right eyes correspond to one another. Another way of stating the problem is: How does the visual system match up the images in the two eyes? This matching of the images is involved in determining depth perception using the cue of binocular disparity. (10)

Corresponding retinal points The points on each retina that would overlap if one retina were slid on top of the other. Receptors at corresponding points send their signals to the same location in the brain. (10)

Cortical magnification Occurs when a disproportionately large area on the cortex is activated by stimulation of a small area on the receptor surface. One example of cortical magnification is the relatively large area of visual cortex that is activated by stimulation of the fovea. An example in the somatosensory system is the large area of somatosensory cortex activated by stimulation of the lips and fingers. (4)

Cortical magnification factor The size of the cortical magnification effect. (4)

Covert attention Attention without looking. Seeing something "out of the corner of your eye" is an example of covert attention. (6)

COVID-19 An acute respiratory illness in humans caused by a coronavirus, originally identified in China in 2019, and becoming a pandemic in 2020. (16)

Crossed disparity Disparity that occurs when one object is being fixated, and is therefore on the horoptor, and another object is located in front of the horoptor, closer to the observer. (10)

CT afferents Unmyelinated nerve fibers found in hairy skin, which have been shown to be involved in social touch. (15)

Cue approach to depth perception The approach to explaining depth perception that focuses on identifying information in the retinal image that is correlated with depth in the scene. Some of the depth cues that have been identified are overlap, relative height, relative size, atmospheric perspective, convergence, and accommodation. (10)

Cutaneous receptive field Area of skin that, when stimulated, influences the firing of a neuron. (15)

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Cutaneous senses The ability to perceive sensations, such as touch and pain, that are based on the stimulation of receptors in the skin. (15)

Dark adaptation Visual adaptation that occurs in the dark, during which the sensitivity to light increases. This increase in sensitivity is associated with regeneration of the rod and cone visual pigments. (3)

Dark adaptation curve The function that traces the time course of the increase in visual sensitivity that occurs during dark adaptation. (3)

Dark-adapted sensitivity The sensitivity of the eye after it has completely adapted to the dark. (3)

Data-based processing Another name for bottom-up processing. Refers to processing that is based on incoming data, as opposed to top-down, or knowledge-based, processing, which is based on prior knowledge. (1)

Decay The decrease in the sound signal that occurs at the end of a tone. (11)

Decibel (dB) A unit that indicates the pressure of a sound stimulus relative to a reference pressure: $dB = 20 \log (p/p_o)$ where p is the pressure of the tone and p_o is the reference pressure. (11)

Decoder A computer program that can predict the most likely stimulus based on the voxel activation patterns that were previously observed in the calibration phase of neural mind reading. (5)

Delay unit A component of the Reichardt detector proposed to explain how neural firing occurs to different directions of movement. The delay unit delays the transmission of nerve impulses as they travel from the receptors toward the brain. (8)

Deletion A cue that provides information about the relative depth of two surfaces. Deletion occurs when a farther object is covered by a nearer object due to sideways movement of an observer relative to the objects. *See also* **Accretion**. (10)

Dendrites Nerve processes on the cell body that receive stimulation from other neurons. (2)

Depolarization When the inside of a neuron becomes more positive, as occurs during the initial phases of the action potential. Depolarization is often associated with the action of excitatory neurotransmitters. (2)

Dermis The layer of skin below the epidermis. (15)

Desaturated Low saturation in chromatic colors as would occur when white is added to a color. For example, pink is not as saturated as red. (9)

Detached retina A condition in which the retina is detached from the back of the eye. (3)

Detection threshold For olfaction the detection threshold is the lowest concentration at which an odorant can be detected. (16)

Deuteranopia A form of dichromatism in which a person is missing the medium-wavelength pigment. A deuteranope perceives blue at short wavelengths, sees yellow at long wavelengths, and has a neutral point at about 498 nm. (9)

Dichotic listening Attention experiment technique involving hearing where *dichotic* refers to presenting different stimuli to the left and right ears. (6)

Dichromat A person who has a form of color deficiency. Dichromats can match any wavelength in the spectrum by mixing two other wavelengths. (9)

Dichromatism A form of color deficiency in which a person has just two types of cone pigment and so can see chromatic colors but confuse some colors that trichromats can distinguish.

Difference threshold The minimum *difference* that must exist *between* two stimuli before we can tell the difference between them. (1)

Direct pathway model of pain The idea that pain occurs when nociceptor receptors in the skin are stimulated and send their signals to the brain. This model does not account for the fact that pain can be affected by other factors in addition to stimulation of the skin. (15)

Direct sound Sound that is transmitted directly from a sound source to the ears. (12)

Discriminative function of touch Functions of the touch system such as sensing details, texture, vibration, and objects. (15)

Dishabituation An increase in responding that occurs when a stimulus is changed. This response is used in testing infants to see whether they can differentiate two stimuli. (9)

Disparity-selective cell *See* **Binocular depth cell**. (10)

Disparity tuning curve A plot of a neuron's response versus the degree of disparity of a visual stimulus. The disparity to which a neuron responds best is an important property of disparity-selective cells, which are also called binocular depth cells. (10)

Dissonance The negative sound quality created when two or more pitches are played together. (13)

Distal stimulus The stimulus "out there," in the external environment. (1)

Distance How far a stimulus is from the observer. In hearing, the distance coordinate specifies how far the sound source is from the listener. (12)

Distributed representation Occurs when a stimulus causes neural activity in a number of different areas of the brain, so the activity is distributed across the brain. (2)

Dopamine Neurotransmitter that is involved in reward-motivated behavior. Dopamine has been associated with the rewarding effects of music. (13)

Dorsal pathway Pathway that conducts signals from the striate cortex to the parietal lobe. The dorsal pathway has also been called the *where*, the *how*, or the *action* pathway by different investigators. (4)

Double dissociation In brain damage, when function A is present and function B is absent in one person, and function A is absent and function B is present in another. Presence of a double dissociation means that the two functions involve different mechanisms and operate independently of one another. (4)

Dual-stream model of speech perception Model that proposes a ventral stream starting in the temporal lobe that is responsible for recognizing speech, and a dorsal stream starting in the parietal lobe that is responsible for linking the acoustic signal to the movements used to produce speech. (14)

Duple meter In Western music, meter in which accents are in multiples of two, such as 12 12 12 or 1234 1234 1234, like a march. (13)

Duplex theory of texture perception The idea that texture perception is determined by both spatial and temporal cues that are detected by two types of receptors. Originally proposed by David Katz and now called the "duplex theory." (15)

Eardrum Another term for the tympanic membrane, the membrane located at the end of the auditory canal that vibrates in response to pressure changes. This vibration is transmitted to the bones of the middle ear. (11)

Early right anterior negativity (ERAN) Physiological "surprise response" experienced by listeners, occurring in the right hemisphere of the brain, in reaction to violations of linguistic or musical syntax. (13)

Echolocation Locating objects by sending out high-frequency pulses and sensing the echo created when these pulses are reflected from objects in the environment. Echolocation is used by bats and dolphins. (10)

Ecological approach to perception This approach focuses on specifying the information in the environment that is used for perception, emphasizing the study of moving observers to determine

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how their movement results in perceptual information that both creates perception and guides further movement. (7)

Edge enhancement An increase in perceived contrast at borders between regions of the visual field. (3)

Effect of the missing fundamental Removing the fundamental frequency and other lower harmonies from a musical tone does not change the tone's pitch. (11)

Electromagnetic spectrum Continuum of electromagnetic energy that extends from very-short-wavelength gamma rays to long-wavelength radio waves. Visible light is a narrow band within this spectrum. (1)

Elevation In hearing, sound locations that are up and down relative to the listener. (12)

Emmert's law A law stating that the size of an afterimage depends on the distance of the surface against which the afterimage is viewed. The farther away the surface, the larger the afterimage appears. (10)

Emotivist approach (to musical emotion) Approach to describing the emotional response to music which proposes that a listener's emotional response to music involves actually feeling the emotions. (13)

Empathy The ability to share and vicariously experience what someone else is feeling. (15)

Endorphin Chemical that is naturally produced in the brain and that causes analgesia. (15)

End-stopped cell A cortical neuron that responds best to lines of a specific length that are moving in a particular direction. (4)

Epidermis The outer layers of the skin, including a layer of dead skin cells. (15)

Equal loudness curve A curve that indicates the sound pressure levels that result in a perception of the same loudness at frequencies across the audible spectrum. (11)

Event A segment of time at a particular location that is perceived by observers to have a beginning and an ending. (8)

Event boundary The point in time when one event ends and another begins. (8)

Event-related potential (ERP) The brain's response to a specific event, such as flashing an image or presenting a tone, as measured with small disc electrodes placed on a person's scalp. (13)

Evolutionary adaptation A function which evolved specifically to aid in survival and reproduction. (13)

Excitatory area Area of a receptive field that is associated with excitation. Stimulation of this area causes an increase in the rate of nerve firing. (3)

Excitatory response The response of a nerve fiber in which the firing rate increases. (2)

Excitatory-center, inhibitory-surround receptive field A center-surround receptive field in which stimulation of the center area causes an excitatory response and stimulation of the surround causes an inhibitory response. (3)

Experience-dependent plasticity A process by which neurons adapt to the specific environment within which a person or animal lives. This is achieved when neurons change their response properties so they become tuned to respond best to stimuli that have been repeatedly experienced in the environment. *See also* **Neural plasticity**; **Selective rearing**. (4)

Experience sampling Technique used to measure the thoughts, feelings, and behaviors of people at various random points in time during the day. This technique has been used to measure the frequency of mind-wandering. (6)

Expertise hypothesis The idea that human proficiency in perceiving certain things can be explained by changes in the brain caused by long exposure, practice, or training. (5)

Exploratory procedures (EPs) People's movements of their hands and fingers while they are identifying three-dimensional objects by touch. (15)

Extinction A condition associated with brain damage in which there is a lack of awareness of what is happening in one side of the visual field. (6)

Extrastriate body area (EBA) An area of the temporal lobe that is activated by pictures of bodies and parts of bodies. (5)

Extrastriate cortex Collective term for visual areas in the occipital lobe and beyond known as V2, V3, V4, and V5. (4)

Eye The eyeball and its contents, which include focusing elements, the retina, and supporting structures. (3)

Falling phase of the action potential In the axon, or nerve fiber, the increase in negativity from +40 mV back to −70 mV (the resting potential level) that occurs during the action potential. This increase in negativity is associated with the flow of positively charged potassium ions (K^+) out of the axon. (2)

False alarm In a signal detection experiment, saying "Yes, I detect the stimulus" on a trial in which the stimulus is not presented (an incorrect response). (Appendix C)

Familiar size A depth cue in which judgment of distance is based on knowledge of the sizes of objects. Epstein's coin experiment illustrated the operation of the cue of familiar size by showing that the relative sizes of the coins influenced perception of the coins' distances. (10)

Farsightedness *See* **Hyperopia**. (3)

Feature detector A neuron that responds selectively to a specific feature of the stimulus such as orientation or direction of motion. (4)

Feature integration theory (FIT) A theory proposed by Anne Treisman to explain how an object is broken down into features and how these features are recombined to result in a perception of the object. (6)

Feature search A visual search task in which a person can find a target by searching for only one feature. An example would be looking for a horizontal green line among vertical green lines. (6)

Figural cue Visual cue that determines how an image is segregated into figure and ground. (5)

Figure When an object is seen as separate from the background (the "ground"), it is called a figure. *See also* **Figure–ground segregation**. (5)

Figure–ground segregation The perceptual separation of an object from its background. (5)

First harmonic *See* **Fundamental frequency**. (11)

Fixation The brief pause of the eye that occurs between eye movements as a person scans a scene. (6)

Flavor The perception that occurs from the combination of taste and olfaction. (16)

Focus of expansion (FOE) The point in the flow pattern caused by observer movement in which there is no expansion. According to J. J. Gibson, the focus of expansion always remains centered on the observer's destination. (7)

Focused attention meditation Common form of meditation in which a person focuses on a specific object, which can be the breath, a sound, a mantra (a syllable, word, or group of words), or a visual stimulus. (6)

Focused attention stage (of perceptual processing) The stage of processing in feature integration theory in which the features are combined. According to Treisman, this stage requires focused attention. (6)

Forced-choice method Method in which two choices are given, and the subject has to pick one. For example, a subject is presented with a weak odorant on one trial, and no odorant on another trial, and has to pick the trial on which the odorant was presented. (16)

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Formant Horizontal band of energy in the speech spectrogram associated with vowels. (14)

Formant transition In the speech stimulus, the rapid shift in frequency that precedes a formant. (14)

Fovea A small area in the human retina that contains only cone receptors. The fovea is located on the line of sight, so that when a person looks at an object, the center of its image falls on the fovea. (3)

Frequency The number of times per second that pressure changes of a sound stimulus repeat. Frequency is measured in Hertz, where 1 Hertz is one cycle per second. (11)

Frequency spectrum A plot that indicates the amplitudes of the various harmonics that make up a complex tone. Each harmonic is indicated by a line that is positioned along the frequency axis, with the height of the line indicating the amplitude of the harmonic. (11)

Frequency tuning curve Curve relating frequency and the threshold intensity for activating an auditory neuron. (11)

Frontal eyes Eyes located in front of the head, so the views of the two eyes overlap. (10)

Frontal lobe Receiving signals from all of the senses, the frontal lobe plays an important role in perceptions that involve the coordination of information received through two or more senses. It also serves functions such as language, thought, memory, and motor functioning. (1)

Frontal operculum cortex An area in the frontal lobe of the cortex that receives signals from the taste system. (16)

Functional connectivity Neural connectivity between two areas of the brain that are activated when carrying out a specific function. (2)

Functional magnetic resonance imaging (fMRI) A brain imaging technique that indicates brain activity in awake, behaving organisms. The fMRI response occurs when the response to a magnetic field changes in response to changes in blood flow in the brain. (2)

Fundamental A pure tone with frequency equal to the fundamental frequency of a complex tone. *See also* **Fundamental frequency**. (11)

Fundamental frequency The first harmonic of a complex tone; usually the lowest frequency in the frequency spectrum of a complex tone. The tone's other components, called higher harmonics, have frequencies that are multiples of the fundamental frequency. (11)

Fusiform face area (FFA) An area in the human inferotemporal (IT) cortex that contains neurons that are specialized to respond to faces. (5)

Ganglion cell A neuron in the retina that receives inputs from bipolar and amacrine cells. The axons of the ganglion cells are the nerve fibers that travel out of the eye in the optic nerve. (3)

Gap fill In music, when after a large jump from one note to another, the next notes of the melody turn around, progressing in the opposite direction, to fill the gap. (13)

Gate control model Melzack and Wall's idea that perception of pain is controlled by a neural circuit that takes into account the relative amount of activity in nociceptors, mechanoreceptors, and central signals. This model has been used to explain how pain can be influenced by factors other than stimulation of receptors in the skin. (15)

Geons According to recognition by components (RBC) theory, individual geometric components that comprise objects. (5)

Gestalt psychology An approach to psychology that developed as a reaction to structuralism. The Gestalt approach proposes principles of perceptual organization and figure–ground segregation and states that "the whole is different than the sum of its parts." (5)

Gist of a scene General description of a scene. People can identify most scenes after viewing them for only a fraction of a second, as when they flip rapidly from one TV channel to another. It takes longer to identify the details within the scene. (5)

Global image features Information that may enable observers to rapidly perceive the gist of a scene. Features associated with specific types of scenes include degree of naturalness, degree of openness, degree of roughness, degree of expansion, and color. (5)

Global optic flow Information for movement that occurs when all elements in a scene move. The perception of global optic flow indicates that it is the observer that is moving and not the scene. (8)

Glomeruli Small structures in the olfactory bulb that receive signals from similar olfactory receptor neurons. One function of each glomerulus is to collect information about a small group of odorants. (16)

Good continuation, principle of A Gestalt principle of perceptual organization that states that points that, when connected, result in straight or smoothly curving lines are seen as belonging together, and that lines tend to be seen in such a way as to follow the smoothest path. (5)

Good figure, principle of *See* **Pragnanz, principle of**. (5)

Gradient of flow In an optic flow pattern, a gradient is created by movement of an observer through the environment. The "gradient" refers to the fact that the optic flow is rapid in the foreground and becomes slower as distance from the observer increases. (7)

Grandmother cell A highly specific type of neuron that fires in response to a specific stimulus, such as a person's grandmother. (2)

Grating acuity (cutaneous) The narrowest spacing of a grooved surface on the skin for which orientation can be accurately judged. *See also* **Two-point threshold**. (15)

Grating acuity (visual) The smallest width of lines for which the orientation of a black and white striped stimulus can be accurately judged. (1)

Grid cells Cells in the entorhinal cortex that fire when an animal is in a particular place in the environment, and which have multiple place fields arranged in a gridlike pattern. (7)

Ground In object perception, the background is called the ground. *See also* **Figure**. (5)

Grouping In perceptual organization, the process by which visual events are "put together" into units or objects. (5)

Habituation procedure Procedure in which a person pays less attention when the same stimulus is presented repeatedly. For example, infants look at a stimulus less and less on each successive trial. *See also* **Dishabituation**. (9)

Hair cells Neurons in the cochlea that contain small hairs, or cilia, that are displaced by vibration of the basilar membrane and fluids inside the inner ear. There are two kinds of hair cells: inner and outer. (11)

Hair cells, inner Auditory receptor cells in the inner ear that are primarily responsible for auditory transduction and the perception of pitch. (11)

Hair cells, outer Auditory receptor cells in the inner ear that amplify the response of inner hair cells by amplifying the vibration of the basilar membrane. (11)

Hand dystonia A condition which causes the fingers to curl into the palm. (15)

Haptic perception The perception of three-dimensional objects by touch. (15)

Harmonics Pure-tone components of a complex tone that have frequencies that are multiples of the fundamental frequency. (11)

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Harmony The qualities of sound (positive or negative) created when two or more pitches are played together. (13)

Head-mounted eye tracking Eye tracking technique in which the perceiver is fitted with two devices: (1) a head-mounted scene camera, which indicates the orientation of the perceiver's head and their general field of view, and (2) an eye camera, which indicates the precise location where the person is looking within that field of view. (6)

Hering's primary colors The colors red, yellow, green, and blue in the color circle. (9)

Hertz (Hz) The unit for designating the frequency of a tone. One Hertz equals one cycle per second. (11)

Hidden hearing loss Hearing loss that occurs at high sound levels, even though the person's thresholds, as indicated by the audiogram, are normal. (11)

Higher harmonics Pure tones with frequencies that are whole-number (2, 3, 4, etc.) multiples of the fundamental frequency. *See also* **Fundamental**; **Fundamental frequency**; **Harmonics**. (11)

Hippocampus Subcortical structure in the brain that is associated with forming and storing memories. (4)

Hit In a signal detection experiment, saying "Yes, I detect a stimulus" on a trial in which the stimulus is present (a correct response). (Appendix C)

Homunculus Latin for "little man"; refers to the topographic map of the body in the somatosensory cortex. (15)

Horizontal cell A neuron that transmits signals laterally across the retina. Horizontal cells synapse with receptors and bipolar cells. (3)

Horopter An imaginary surface that passes through the point of fixation. Images caused by a visual stimulus on this surface fall on corresponding points on the two retinas. (10)

***How* pathway** *See* **Dorsal pathway**. (4)

Hue The experience of a chromatic color, such as red, green, yellow, or blue, or combinations of these colors. (9)

Hue cancellation Procedure in which a subject is shown a monochromatic reference light and is asked to remove, or "cancel," the one of the colors in the reference light by adding a second wavelength. This procedure was used by Hurvich and Jameson in their research on opponent-process theory. (9)

Hue scaling Procedure in which participants are given colors from around the hue circle and told to indicate the proportions of red, yellow, blue, and green that they perceive in each color. (9)

Hypercolumn In the striate cortex, unit proposed by Hubel and Wiesel that combines location, orientation, and ocular dominance columns that serve a specific area on the retina. (4)

Hyperopia A condition causing poor vision in which people can see objects that are far away but do not see near objects clearly. Also called farsightedness. (3)

Hyperpolarization When the inside of a neuron becomes more negative. Hyperpolarization is often associated with the action of inhibitory neurotransmitters. (2)

Illumination edge The border between two areas created by different light intensities in the two areas. (9)

Illusory conjunction Illusory combination of features that are perceived when stimuli containing a number of features are presented briefly and under conditions in which focused attention is difficult. For example, presenting a red square and a blue triangle could potentially create the perception of a red triangle. (6)

Illusory contour Contour that is perceived even though it is not present in the physical stimulus. (5)

Illusory motion Perception of motion when there actually is none. *See also* **Apparent motion**. (8)

Image displacement signal (IDS) In corollary discharge theory, the signal that occurs when an image moves across the visual receptors. (6)

Implied motion When a still picture depicts an action that involves motion, so that an observer could potentially extend the action depicted in the picture in his or her mind based on what will most likely happen next. (8)

Inattentional blindness A situation in which a stimulus that is not attended is not perceived, even though the person is looking directly at it. (6)

Incus The second of the three ossicles of the middle ear. It transmits vibrations from the malleus to the stapes. (11)

Indirect sound Sound that reaches a listener's ears after being reflected from a surface such as a room's walls. (12)

Induced motion The illusory movement of one object that is caused by the movement of another object that is nearby. (8)

Infant-directed speech (IDS) Also called "motherese" (or more recently, "parentese"), or "baby talk," a patter of speech that has special characteristics that both attract an infant's attention and make it easier for the infant to recognize individual words. (13)

Inferior colliculus A nucleus in the hearing system along the pathway from the cochlea to the auditory cortex. The inferior colliculus receives inputs from the superior olivary nucleus. (11)

Inferotemporal (IT) cortex An area of the brain outside Area V1 (the striate cortex), involved in object perception and facial recognition. (4)

Inflammatory pain Pain caused by damage to tissues, inflammation of joints, or tumor cells. This damage releases chemicals that create an "inflammatory soup" that activates nociceptors. (15)

Inhibitory area Area of a receptive field that is associated with inhibition. Stimulation of this area causes a decrease in the rate of nerve firing. (3)

Inhibitory response Occurs when a neuron's firing rate decreases due to inhibition from another neuron. (2)

Inhibitory-center, excitatory-surround receptive field A center-surround receptive field in which stimulation of the center causes an inhibitory response and stimulation of the surround causes an excitatory response. (3)

Inner ear The innermost division of the ear, containing the cochlea and the receptors for hearing. (11)

Inner hair cells *See* **Hair cells, inner**. (11)

Insula An area in the frontal lobe of the cortex that receives signals from the taste system and is also involved in the affective component of the perception of pain. (16)

Interaural level difference (ILD) The difference in the sound pressure (or *level*) between the left and right ears. This difference creates an acoustic shadow for the far ear. The ILD provides a cue for sound localization for high-frequency sounds. (12)

Interaural time difference (ITD) When a sound is positioned closer to one ear than to the other, the sound reaches the close ear slightly before reaching the far ear, so there is a difference in the time of arrival at the two ears. The ITD provides a cue for sound localization. (12)

Inter-onset interval In music, the time between the onset of each note. (13)

Interpersonal touching One person touching another person. *See also* **social touch**. (15)

Interval In music, the spacing between notes. (13)

Invariant information Environmental properties that do not change as the observer moves relative to an object or scene. For example, the spacing, or texture, of the elements in a homogenous texture gradient does not change as the observer moves on the gradient. The texture of the gradient therefore supplies invariant information for depth perception. (7)

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Inverse projection problem The idea that a particular image on the retina could have been caused by an infinite number of different objects. This means that the retinal image does not unambiguously specify a stimulus. (5)

Ions Charged molecules. Sodium (Na^+), potassium (K^+), and chlorine (Cl^-) are the main ions found within nerve fibers and in the liquid that surrounds nerve fibers. (2)

Ishihara plate A display of colored dots used to test for the presence of color deficiency. The dots are colored so that people with normal (trichromatic) color vision can perceive numbers in the plate, but people with color deficiency cannot perceive these numbers or perceive different numbers than someone with trichromatic vision. (9)

Isolated congenital anosmia (ICA) A condition in which a person is born without a sense of smell. (16)

Isomerization Change in shape of the *retinal* part of the visual pigment molecule that occurs when the molecule absorbs a quantum of light. Isomerization triggers the enzyme cascade that results in transduction from light energy to electrical energy in the retinal receptors. (3)

ITD detector Interaural time difference detector. Neurons in the Jeffress neural coincidence model that fire when signals reach them from the left and right ears. Each ITD detector is tuned to respond to a specific time delay between the two signals, and so provides information about possible locations of a sound source. (12)

ITD tuning curve A plot of the neuron's firing rate against the ITD (interaural time difference). (12)

Jeffress model The neural mechanism of auditory localization that proposes that neurons are wired to each receive signals from the two ears, so that different neurons fire to different interaural time differences (ITD). (12)

Kinesthesis The sense that enables us to feel the motions and positions of the limbs and body. (15)

Knowledge Any information that the perceiver brings to a situation. *See also* **Top-down processing**. (1)

Knowledge-based processing *See* **Top-down processing**. (15)

Landmark Object on a route that serves as a cue to indicate where to turn; a source of information for wayfinding. (7)

Landmark discrimination problem The behavioral task used in Ungerleider and Mishkin's experiment in which they provided evidence for the dorsal, or *where*, visual processing stream. Monkeys were required to respond to a previously indicated location. (4)

Lateral eyes Eyes located on opposite sides of an animal's head, as in the pigeon and the rabbit, so the views of the two eyes do not overlap or overlap only slightly. (10)

Lateral geniculate nucleus (LGN) The nucleus in the thalamus that receives inputs from the optic nerve and, in turn, communicates with the cortical receiving area for vision. (4)

Lateral inhibition Inhibition that is transmitted laterally across a nerve circuit. In the retina, lateral inhibition is transmitted by the horizontal and amacrine cells. (3)

Lateral occipital complex (LOC) Area of the brain that is active when a person views any kind of object—such as an animal, face, house, or tool—but not when they view a texture, or an object with the parts scrambled. (5)

Leisure noise Noise associated with leisure activities such as listening to music, hunting, and woodworking. Exposure to high levels of leisure noise for extended periods can cause hearing loss. (11)

Lens The transparent focusing element of the eye through which light passes after passing through the cornea and the aqueous humor. The lens's change in shape to focus at different distances is called accommodation. (3)

Level Short for sound pressure level or sound level. Indicates the decibels or sound pressure of a sound stimulus. (11)

Light-adapted sensitivity The sensitivity of the eye when in the light-adapted state. Usually taken as the starting point for the dark adaptation curve because it is the sensitivity of the eye just before the lights are turned off. (3)

Light-from-above assumption The assumption that light usually comes from above, which influences our perception of form in some situations. (5)

Lightness The perception of shades ranging from white to gray to black. (9)

Lightness constancy The constancy of our perception of an object's lightness under different intensities of illumination. (9)

Likelihood (Bayes) In Bayesian inference, the extent to which the available evidence is consistent with a particular outcome. (5)

Likelihood principle (Helmholtz) The idea proposed by Helmholtz that we perceive the object that is *most likely* to have caused the pattern of stimuli we have received. (5)

Limits, method of A psychophysical method for measuring threshold in which the experimenter presents sequences of stimuli in ascending and descending order. (1)

Local disturbance in the optic array Occurs when one object moves relative to the environment, so that the stationary background is covered and uncovered by the moving object. This local disturbance indicates that the object is moving relative to the environment. (8)

Location column A column in the visual cortex that contains neurons with the same receptive field locations on the retina. (4)

Location cues In hearing, characteristics of the sound reaching the listener that provide information regarding the location of a sound source. (12)

Loudness The quality of sound that ranges from soft to loud. For a tone of a particular frequency, loudness usually increases with increasing decibels. (11)

Mach bands Light and dark bands perceived at light–dark borders. (3)

Macrosmatic Having a keen sense of smell; usually important to an animal's survival. (16)

Macular degeneration A clinical condition that causes degeneration of the macula, an area of the retina that includes the fovea and a small surrounding area. (3)

Magnetic resonance imaging (MRI) Brain scanning technique that makes it possible to create images of structures within the brain. (2)

Magnitude estimation A psychophysical method in which the subject assigns numbers to a stimulus that are proportional to the subjective magnitude of the stimulus. (1)

Malleus The first of the ossicles of the middle ear. Receives vibrations from the tympanic membrane and transmits these vibrations to the incus. (11)

Manner of articulation How a speech sound is produced by interaction of the articulators—the mouth, tongue, and lips—during production of the sound. (14)

McGurk effect *See* **Audiovisual speech perception**. (14)

Mechanoreceptor Receptor that responds to mechanical stimulation of the skin, such as pressure, stretching, or vibration. (15)

Medial geniculate nucleus An auditory nucleus in the thalamus that is part of the pathway from the cochlea to the auditory cortex. The medial geniculate nucleus receives inputs from the inferior colliculus and transmits signals to the auditory cortex. (11)

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Medial lemniscal pathway A pathway in the spinal cord that transmits signals from the skin toward the thalamus. (15)

Meditation A practice that originated in Buddhist and Hindu cultures, which involves different ways of engaging the mind. *See* **Focused-attention meditation**. (6)

Meissner corpuscle (RA1) A receptor in the skin, associated with RA1 mechanoreceptors. It has been proposed that the Meissner corpuscle is important for perceiving tactile slip and for controlling the force needed to grip objects. (15)

Melodic channeling *See* **Scale illusion**. (12)

Melody The experience of a sequence of pitches as belonging together. Usually refers to the way notes follow one another in a song or musical composition. (13)

Melody schema A representation of a familiar melody that is stored in a person's memory. Existence of a melody schema makes it more likely that the tones associated with a melody will be perceptually grouped. (12)

Memory color The idea that an object's characteristic color influences our perception of that object's color. (9)

Merkel receptor (SA1) A disk-shaped receptor in the skin associated with slowly adapting fibers and the perception of fine details. (15)

Metamerism The situation in which two physically different stimuli are perceptually identical. In vision, this refers to two lights with different wavelength distributions that are perceived as having the same color. (9)

Metamers Two lights that have different wavelength distributions but are perceptually identical. (9)

Meter In music, organization of beats into bars or measures, with the first beat in each bar often being accented. There are two basic kinds of meter in Western music: duple meter, in which accents are in multiples of two, such as 12 12 12 or 1234 1234 1234, like a march; and triple meter, in which accents are in groups of three, such as 123 123 123, as in a waltz. (13)

Method of adjustment *See* **Adjustment, method of**. (1)

Method of constant stimuli *See* **Constant stimuli, method of**. (1)

Method of limits *See* **Limits, method of**. (1)

Metrical structure The pattern of beats indicated by a musical time signature like 2:4, 4:4, or 3:4. Musicians often accentuate initial notes of a measure by using a stronger attack or by playing them louder or longer. (13)

Microneurography Technique used to record neural signals that involves inserting a metal electrode with a very fine tip just under the skin. (15)

Microsmatic Having a weak sense of smell. This usually occurs in animals, such as humans, in which the sense of smell is not crucial for survival. (16)

Microspectrophotometry A technique in which a narrow beam of light is directed into a single visual receptor. This technique makes it possible to determine the pigment absorption spectra of single receptors. (9)

Microstimulation A procedure in which a small electrode is inserted into the cortex and an electrical current passed through the electrode activates neurons near the tip of the electrode. This procedure has been used to determine how activating specific groups of neurons affects perception. (8)

Middle ear The small air-filled space between the auditory canal and the cochlea that contains the ossicles. (11)

Middle-ear muscles Muscles attached to the ossicles in the middle ear. The smallest skeletal muscles in the body, they contract in response to very intense sounds and dampen the vibration of the ossicles. (11)

Middle temporal (MT) area Brain region in the temporal lobe that contains many directionally selective neurons. (8)

Mild cognitive impairment Cognitive impairments that extend beyond those associated with normal aging, but which often do not interfere with activities of daily living. Often is a precursor to more serious conditions such as Alzheimer's disease. (16)

Mind–body problem One of the most famous problems in science: How do physical processes such as nerve impulses or sodium and potassium molecules flowing across membranes (the body part of the problem) become transformed into the richness of perceptual experience (the mind part of the problem)? (2)

Mind wandering Non-task-oriented mental activity. Also called daydreaming. (6)

Mirror neuron Neuron in the premotor area of the monkey's cortex that responds when the monkey grasps an object and also when the monkey observes someone else (another monkey or the experimenter) grasping the object. There is also evidence for mirror-neuron-like activity in the human brain. *See also* **Audiovisual mirror neuron**. (7)

Mirror neuron system Network of neurons hypothesized to play a role in creating mirror neurons. (7)

Misapplied size constancy scaling A principle, proposed by Richard Gregory, that when mechanisms that help maintain size constancy in the three-dimensional world are applied to two-dimensional pictures, an illusion of size sometimes results. (10)

Miss In a signal detection experiment, saying "No, I don't detect a stimulus" on a trial in which the stimulus is present (an incorrect response). (Appendix C)

Modularity The idea that specific areas of the cortex are specialized to respond to specific types of stimuli. (2)

Module A structure that processes information about a specific behavior or perceptual quality. Often identified as a structure that contains a large proportion of neurons that respond selectively to a particular quality, such as the fusiform face area, which contains many neurons that respond selectively to faces. (2)

Monochromat A person who is completely color-blind and therefore sees everything as black, white, or shades of gray. A monochromat can match any wavelength in the spectrum by adjusting the intensity of any other wavelength. Monochromats generally have only one type of functioning receptors, usually rods. (9)

Monochromatic light Light that contains only a single wavelength. (3)

Monochromatism Rare form of color blindness in which the absence of cone receptors results in perception only of shades of lightness (white, gray, and black), with no chromatic color present. (9)

Monocular cue Depth cue—such as overlap, relative size, relative height, familiar size, linear perspective, movement parallax, and accommodation—that can work when we use only one eye. (10)

Moon illusion An illusion in which the moon appears to be larger when it is on or near the horizon than when it is high in the sky. (10)

Motion aftereffect An illusion that occurs after a person views a moving stimulus and then sees movement in the opposite direction when viewing a stationary stimulus immediately afterward. *See also* **Waterfall illusion**. (8)

Motion parallax A depth cue. As an observer moves, nearby objects appear to move rapidly across the visual field whereas far objects appear to move more slowly. (10)

Motor signal (MS) In corollary discharge theory, the signal that is sent to the eye muscles when the observer moves or tries to move his or her eyes. (6)

Motor theory of speech perception A theory that proposes a close link between how speech is perceived and how it is produced. The idea behind this theory is that when we *hear* a particular speech sound, this activates the motor mechanisms that are responsible for *producing* that sound, and it is the activation of these motor mechanisms that enable us to perceive the sound. (14)

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Müller-Lyer illusion An illusion in which two lines of equal length appear to be of different lengths because of the addition of "fins" to the ends of the lines. (10)

Multimodal The involvement of a number of different senses in determining perception. For example, speech perception can be influenced by information from a number of different senses, including audition, vision, and touch. (14)

Multimodal interactions Interactions that involve more than one sense or quality. (16)

Multimodal nature of pain The fact that the experience of pain has both sensory and emotional components. (15)

Multisensory interaction Use of a combination of senses. An example for vision and hearing is seeing a person's lips move while listening to the person speak. (12)

Multivoxel pattern analysis (MVPA) In neural mind reading, a technique in which the pattern of activated voxels is used to determine what a person is perceiving or thinking. (5)

Munsell color system Depiction of hue, saturation, and value developed by Albert Munsell in the early 1900s in which different hues are arranged around the circumference of a cylinder with perceptually similar hues placed next to each other. (9)

Music Sound organized in a way that, in traditional Western music, creates a melody. (13)

Music-evoked autobiographical memory (MEAM) Memory triggered by listening to music. MEAMs are often associated with strong emotions like happiness and nostalgia, but can also be associated with sad emotions. (13)

Musical phrases How notes are perceived as forming segments like phrases in language. (13)

Musical syntax Rules that specify how notes and chords are combined in music. (13)

Myopia An inability to see distant objects clearly. Also called nearsightedness. (3)

Naloxone A substance that inhibits the activity of opiates. It is hypothesized that naloxone also inhibits the activity of endorphins and therefore can have an effect on pain perception. (15)

Nasal pharynx A passageway that connects the mouth cavity and the nasal cavity. (16)

Nearsightedness *See* **Myopia**. (3)

Nerve fiber In most sensory neurons, the long part of the neuron that transmits electrical impulses from one point to another. Also called the axon. (2)

Neural circuit A number of neurons that are connected by synapses. (3)

Neural convergence Synapsing of a number of neurons onto one neuron. (3)

Neural mind reading Using a neural response, usually brain activation measured by fMRI, to determine what a person is perceiving or thinking. (5)

Neural plasticity The capacity of the nervous system to change in response to experience. Examples are how early visual experience can change the orientation selectivity of neurons in the visual cortex and how tactile experience can change the sizes of areas in the cortex that represent different parts of the body. *See also* **Experience-dependent plasticity**; **Selective rearing**. (4)

Neural processing Operations that transform electrical signals within a network of neurons or that transform the response of individual neurons. (1)

Neurogenesis The cycle of birth, development, and death of a neuron. This process occurs for the receptors for olfaction and taste. (16)

Neuron The structure that transmits electrical signals in the body. Key components of neurons are the cell body, dendrites, and the axon or nerve fiber. (2)

Neuropathic pain Pain caused by lesions or other damage to the nervous system. (15)

Neuropsychology The study of the behavioral effects of brain damage in humans. (2)

Neurotransmitter A chemical stored in synaptic vesicles that is released in response to a nerve impulse and has an excitatory or inhibitory effect on another neuron. (2)

Neutral point The wavelength at which a dichromat perceives gray. (9)

Nocebo effect A negative placebo effect, characterized by a negative response to negative expectations. (15)

Nociceptive pain This type of pain, which serves as a warning of impending damage to the skin, is caused by activation of receptors in the skin called nociceptors. (15)

Nociceptor A fiber that responds to stimuli that are damaging to the skin. (15)

Noise A sound stimulus that contains many random frequencies. (11)

Noise In signal detector theory, noise is all of the stimuli in the environment other than the signal. (Appendix C)

Noise-induced hearing loss A form of sensorineural hearing loss that occurs when loud noises cause degeneration of the hair cells. (11)

Noise-vocoded speech A procedure in which the speech signal is divided into different frequency bands and then noise is added to each band. (14)

Noncorresponding points Two points, one on each retina, that would not overlap if the retinas were slid onto each other. Also called disparate points. (10)

Nonspectral colors Colors that do not appear in the spectrum because they are mixtures of other colors. An example is magenta, which is a mixture of red and blue. (9)

Novelty-preference procedure A procedure used to study infant color vision in which two side-by-side squares of different colors are presented and the infant's looking time to the two squares is measured to determine whether they can tell the difference between them. (9)

Nucleus accumbens Brain structure closely associated with the neurotransmitter dopamine, which is released into the nucleus accumbens in response to rewarding stimuli. (13)

Nucleus of the solitary tract The nucleus in the brain stem that receives signals from the tongue, the mouth, and the larynx transmitted by the chorda tympani, glossopharyngeal, and vagus nerves. (16)

Object discrimination problem The behavioral task used in Ungerleider and Mishkin's experiment in which they provided evidence for the ventral, or *what*, visual processing stream. Monkeys were required to respond to an object with a particular shape. (4)

Object recognition The ability to identify objects. (5)

Oblique effect Enhanced sensitivity to vertically and horizontally oriented visual stimuli compared to obliquely oriented (slanted) stimuli. This effect has been demonstrated by measuring both perception and neural responding. (1)

Occipital lobe A lobe at the back of the cortex that is the site of the cortical receiving area for vision. (1)

Occlusion Depth cue in which one object hides or partially hides another object from view, causing the hidden object to be perceived as being farther away. A monocular depth cue. (10)

Octave Tones that have frequencies that are binary multiples of each other (2, 4, etc.). For example, an 800-Hz tone is one octave above a 400-Hz tone. (11)

Oculomotor cue Depth cue that depends on our ability to sense the position of our eyes and the tension in our eye muscles. Accommodation and convergence are oculomotor cues. (10)

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Odor map. *See* **Chemotopic map**. (16)

Odor object The source of an odor, such as coffee, bacon, a rose, or car exhaust. (16)

Odor-evoked autobiographical memory Memories about events from a person's life that are elicited by odors. (16)

Odotoptic map. *See* **Chemotopic map**. (16)

Olfaction The sense of smell. Usually results from stimulation of receptors in the olfactory mucosa. (16)

Olfactory bulb The structure that receives signals directly from the olfactory receptors. The olfactory bulb contains glomeruli, which receive these signals from the receptors. (16)

Olfactory mucosa The region inside the nose that contains the receptors for the sense of smell. (16)

Olfactory receptor A protein string that responds to odor stimuli. (16)

Olfactory receptor neurons (ORNs) Sensory neurons located in the olfactory mucosa that contain the olfactory receptors. (16)

Ommatidium A structure in the eye of the *Limulus* that contains a small lens, located directly over a visual receptor. The *Limulus* eye is made up of hundreds of these ommatidia. The *Limulus* eye has been used for research on lateral inhibition because its receptors are large enough so that stimulation can be applied to individual receptors. (3)

Operant conditioning A type of learning in which behavior is controlled by rewards, called reinforcements, that follow behaviors. (6)

Opioid A chemical such as opium, heroin, and other molecules with related structures that reduce pain and induce feelings of euphoria. (15)

Opponent neuron A neuron that has an excitatory response to wavelengths in one part of the spectrum and an inhibitory response to wavelengths in the other part of the spectrum. (9)

Opponent-process theory of color vision A theory originally proposed by Hering, which claimed that our perception of color is determined by the activity of two opponent mechanisms: a blue–yellow mechanism and a red–green mechanism. The responses to the two colors in each mechanism oppose each other, one being an excitatory response and the other an inhibitory response. In addition, this theory also includes a black–white mechanism, which is concerned with the perception of brightness. *See also* **Opponent neuron**. (9)

Optic array The structured pattern of light created by the presence of objects, surfaces, and textures in the environment. (8)

Optic chiasm An x-shaped bundle of fibers on the underside of the brain, where nerve fibers activated by stimulation of one side of the visual field cross over to the opposite side of the brain. (4)

Optic flow The flow of stimuli in the environment that occurs when an observer moves relative to the environment. Forward movement causes an expanding optic flow, whereas backward movement causes a contracting optic flow. Some researchers use the term *optic flow field* to refer to this flow. (7)

Optic nerve Bundle of nerve fibers that carry impulses from the retina to the lateral geniculate nucleus and other structures. Each optic nerve contains about 1 million ganglion cell fibers. (3)

Oral capture The condition in which sensations from both olfaction and taste are perceived as being located in the mouth. (16)

Orbitofrontal cortex An area in the frontal lobe, near the eyes, that receives signals originating in the olfactory receptors. Also known as the secondary olfactory cortex. (16)

Organ of Corti The major structure of the cochlear partition, containing the basilar membrane, the tectorial membrane, and the receptors for hearing. (11)

Orientation column A column in the visual cortex that contains neurons with the same orientation preference. (4)

Orientation tuning curve A function relating the firing rate of a neuron to the orientation of the stimulus. (4)

Ossicles Three small bones in the middle ear that transmit vibrations from the outer to the inner ear. (11)

Outer ear The pinna and the auditory canal. (11)

Outer hair cells *See* **Hair cells, outer**. (11)

Outer segment Part of the rod and cone visual receptors that contains the light-sensitive visual pigment molecules. (3)

Output unit A component of the Reichardt detector that compares signals received from two or more neurons. According to Reichardt's model, activity in the output unit is necessary for motion perception. (8)

Oval window A small, membrane-covered hole in the cochlea that receives vibrations from the stapes. (11)

Overt attention Attention that involves looking directly at the attended object. (6)

Pacinian corpuscle (RA2 or PC) A receptor with a distinctive elliptical shape associated with RA2 mechanoreceptors. It transmits pressure to the nerve fiber inside it only at the beginning or end of a pressure stimulus and is responsible for our perception of vibration and fine textures when moving the fingers over a surface. (15)

Papillae Ridges and valleys on the tongue, some of which contain taste buds. There are four types of papillae: filiform, fungiform, foliate, and circumvallate. (16)

Parahippocampal place area (PPA) An area in the temporal lobe that is activated by indoor and outdoor scenes. (5)

Parietal lobe A lobe at the top of the cortex that is the site of the cortical receiving area for touch and is the termination point of the dorsal (*where* or *how*) stream for visual processing. (1)

Parietal reach region (PRR) A network of areas in the parietal cortex that contains neurons that are involved in reaching behavior. (7)

Partial color constancy A type of color constancy that occurs when changing an object's illumination causes a change in perception of the object's hue, but less change than would be expected based on the change in the wavelengths of light reaching the eye. Note that in complete color constancy, changing an object's illumination causes no change in the object's hue. (9)

Passive touch A situation in which a person passively receives tactile stimulation. *See also* **Active touch**. (15)

Payoffs A system of rewards and punishments used to influence a participant's motivation in a signal detection experiment. (Appendix C)

Perceived contrast The perceived difference in the appearance of light and dark bars. (6)

Perceived magnitude A perceptual measure of stimuli, such as light or sound, that indicates the magnitude of experience. (1)

Perception Conscious sensory experience. (1)

Perceptual organization The process by which small elements become perceptually grouped into larger objects. (5)

Perceptual process A sequence of steps leading from the environment to perception of a stimulus, recognition of the stimulus, and action with regard to the stimulus. (1)

Periodic sound A sound stimulus in which the pattern of pressure changes repeats. (11)

Periodic waveform For the stimulus for hearing, a pattern of repeating pressure changes. (11)

Peripheral retina The area of retina outside the fovea. (3)

Permeability A property of a membrane that refers to the ability of molecules to pass through it. If the permeability to a molecule is high, the molecule can easily pass through the membrane. (2)

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Persistence of vision A phenomenon in which perception of any stimulus persists for about 250 ms after the stimulus is physically terminated. (5)

Perspective convergence The perception that parallel lines in the distance converge as distance increases. (10)

Phantom limb A person's continued perception of a limb, such as an arm or a leg, even though the limb has been amputated. (15)

Phase locking Firing of auditory neurons in synchrony with the phase of an auditory stimulus. (11)

Phenomenological report Method of determining the relationship between stimuli and perception in which the observer describes what he or she perceives. (1)

Phoneme The shortest segment of speech that, if changed, changes the meaning of a word. (14)

Phonemic restoration effect An effect that occurs in speech perception when listeners perceive a phoneme in a word even though the acoustic signal of that phoneme is obscured by another sound, such as white noise or a cough. (14)

Phonetic boundary The voice onset time when perception changes from one speech category to another in a categorical perception experiment. (14)

Phonetic feature Cues associated with how a phoneme is produced by the articulators. (14)

Photoreceptors The receptors for vision. (3)

Phrenology Belief that different mental faculties could be mapped onto different brain areas based on the bumps and contours on a person's skull. (2)

Physical regularities Regularly occurring physical properties of the environment. For example, there are more vertical and horizontal orientations in the environment than oblique (angled) orientations. (5)

Physical-social pain overlap hypothesis Proposal that pain resulting from negative social experiences is processed by some of the same neural circuitry that processes physical pain. (15)

Physiology–behavior relationship Relationship between physiological responses and behavioral responses. (1)

Pictorial cue Monocular depth cue, such as overlap, relative height, and relative size, that can be depicted in pictures. (10)

Pinna The part of the ear that is visible on the outside of the head. (11)

Piriform cortex (PC) An area under the temporal lobe that receives signals from glomeruli in the olfactory bulb. Also called the primary olfactory area. (16)

Pitch The quality of sound, ranging from low to high, that is most closely associated with the frequency of a tone. (11)

Pitch neuron A neuron that responds to stimuli associated with a specific pitch. These neurons fire to the pitch of a complex tone even if the first harmonic or other harmonics of the tone are not present. (11)

Place cells Neurons that fire only when an animal is in a certain place in the environment. (7)

Place field Area of the environment within which a place cell fires. (7)

Place of articulation In speech production, the locations of articulation. *See* **Manner of articulation**. (14)

Place theory of hearing The proposal that the frequency of a sound is indicated by the place along the organ of Corti at which nerve firing is highest. Modern place theory is based on Békésy's traveling wave theory of hearing. (11)

Placebo A substance that a person believes will relieve symptoms such as pain but that contains no chemicals that actually act on these symptoms. (15)

Placebo effect A relief from symptoms resulting from a substance that has no pharmacological effect. *See also* **Placebo**. (15)

Point-light walker A biological motion stimulus created by placing lights at a number of places on a person's body and having an observer view the moving-light stimulus that results as the person moves in the dark. (8)

Ponzo illusion An illusion of size in which two objects of equal size that are positioned between two converging lines appear to be different in size. Also called the railroad track illusion. (10)

Population coding Representation of a particular object or quality by the pattern of firing of a large number of neurons. (2)

Posterior belt area Posterior (toward the back of the brain) area of the belt area, which is an area in the temporal lobe involved in auditory processing. (12)

Power function A mathematical function of the form $P = KS^n$, where P is perceived magnitude, K is a constant, S is the stimulus intensity, and n is an exponent. (Appendix B)

Pragnanz, principle of A Gestalt principle of perceptual organization that states that every stimulus pattern is seen in such a way that the resulting structure is as simple as possible. Also called the *principle of good figure* or the *principle of simplicity*. (5)

Preattentive processing Hidden processing that happens within a fraction of a second, below one's level of awareness. (6)

Preattentive stage (of perceptual processing) An automatic and rapid stage of processing, proposed by Treisman's feature integration theory, during which a stimulus is decomposed into individual features. (6)

Precedence effect When two identical or very similar sounds reach a listener's ears separated by a time interval of less than about 50 to 100 ms, the listener hears the first sound that reaches his or her ears. (12)

Precueing A procedure in which a cue stimulus is presented to direct an observer's attention to a specific location where a test stimulus is likely to be presented. This procedure was used by Posner to show that attention enhances the processing of a stimulus presented at the cued location. (6)

Predictive coding A theory that describes how the brain uses our past experiences to predict what we will perceive. (5)

Predictive remapping of attention Process in which attention begins shifting toward a target just before the eye begins moving toward it, enabling the perceiver to experience a stable, coherent scene. (6)

Preferential looking technique A technique used to measure perception in infants. Two stimuli are presented, and the infant's looking behavior is monitored for the amount of time the infant spends viewing each stimulus. (3)

Presbycusis A form of sensorineural hearing loss that occurs as a function of age and is usually associated with a decrease in the ability to hear high frequencies. Since this loss also appears to be related to exposure to environmental sounds, it is also called *sociocusis*. (11)

Presbyopia The inability of the eye to accommodate due to a hardening of the lens and a weakening of the ciliary muscles. It occurs as people get older. (3)

Primary auditory cortex (A1) An area of the temporal lobe that receives signals via nerve fibers from the medial geniculate nucleus in the thalamus. (12)

Primary olfactory area A small area under the temporal lobe that receives signals from glomeruli in the olfactory bulb. Also called the piriform cortex. (16)

Primary receiving area Area of the cerebral cortex that first receives most of the signals initiated by a sense's receptors. For example, the occipital cortex is the site of the primary receiving area for vision, and the temporal lobe is the site of the primary receiving area for hearing. (1)

Primary somatosensory cortex (SI) Area of the cortex in the parietal lobe that receives signals that originate from the body and stimulation of the skin. (15)

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Principle of common fate *See* **Common fate, principle of**. (5)
Principle of common region *See* **Common region, principle of**. (5)
Principle of good continuation *See* **Good continuation, principle of**. (5)
Principle of good figure *See* **Pragnanz, principle of**. (5)
Principle of pragnanz *See* **Pragnanz, principle of**. (5)
Principle of proximity (nearness) *See* **Proximity, principle of**. (5)
Principle of representation *See* **Representation, principle of**. (1)
Principle of similarity *See* **Similarity, principle of**. (5)
Principle of simplicity *See* **Pragnanz, principle of**. (5)
Principle of transformation *See* **Transformation, principle of**. (1)
Principle of uniform connectedness *See* **Uniform connectedness, principle of**. (5)
Principle of univariance *See* **Univariance, principle of**. (9)
Principles of perceptual organization Principles that describe how elements in a scene become grouped together. Many of these principles were originally proposed by the Gestalt psychologists, but new principles have also been proposed by recent researchers. (5)
Prior probability (or prior) In Bayesian inference, a person's initial estimate of the probability of an outcome. *See also* **Bayesian inference**. (5)
Propagated response A response, such as a nerve impulse, that travels all the way down the nerve fiber without decreasing in amplitude. (2)
Proprioception The sensing of the position of the limbs. (7)
Prosopagnosia A form of visual agnosia in which the person can't recognize faces. (5)
Protanopia A form of dichromatism in which a protanope is missing the long-wavelength pigment, and perceives short-wavelength light as blue and long-wavelength light as yellow. (9)
Proust effect The elicitation of memories through taste and olfaction. Named for Marcel Proust, who described how the taste and smell of a tea-soaked madeleine cake unlocked childhood memories. (16)
Proximal stimulus The stimulus on the receptors. In vision, this would be the image on the retina. (1)
Proximity, principle of A Gestalt principle of perceptual organization that states that things that are near to each other appear to be grouped together. Also called the principle of nearness. (5)
Psychophysics Traditionally, the term *psychophysics* refers to quantitative methods for measuring the relationship between properties of the stimulus and the subject's experience. In this book, all methods that are used to determine the relationship between stimuli and perception will be broadly referred to as pychophysical methods. (1)
Pupil The opening through which light reflected from objects in the environment enters the eye. (3)
Pure tone A tone with pressure changes that can be described by a single sine wave. (11)
Purkinje shift The shift from cone spectral sensitivity to rod spectral sensitivity that takes place during dark adaptation. *See also* **Spectral sensitivity**. (3)

RA1 fiber Fiber in the skin associated with Meissner corpuscles that adapts rapidly to stimuli and fires only briefly when a tactile stimulus is presented. (15)
RA2 fiber Fiber in the skin associated with Pacinian corpuscle receptors that is located deeper in the skin than RA1 fibers. (15)
Random-dot stereogram A pair of stereoscopic images made up of random dots. When one section of this pattern is shifted slightly in one direction, the resulting disparity causes the shifted section to appear above or below the rest of the pattern when the patterns are viewed in a stereoscope. (10)
Rapidly adapting (RA) fiber Fiber in the cutaneous system that adapts rapidly to a stimulus and so responds briefly to tactile stimulation. (15)
Ratio principle A principle stating that two areas that reflect different amounts of light will have the same perceived lightness if the ratios of their intensities to the intensities of their surroundings are the same. (9)
Rat–man demonstration The demonstration in which presentation of a "ratlike" or "manlike" picture influences an observer's perception of a second picture, which can be interpreted either as a rat or as a man. This demonstration illustrates an effect of top-down processing on perception. (1)
Reaction time The time between presentation of a stimulus and an observer's or listener's response to the stimulus. Reaction time is often used in experiments as a measure of speed of processing. (1)
Real motion The physical movement of a stimulus. Contrasts with *apparent motion.* (8)
Receiver operating characteristic (ROC) curve A graph in which the results of a signal detection experiment are plotted as the proportion of hits versus the proportion of false alarms for a number of different response criteria. (Appendix C)
Receptive field A neuron's receptive field is the area on the receptor surface (the retina for vision; the skin for touch) that, when stimulated, affects the firing of that neuron. (3)
Receptor site Small area on the postsynaptic neuron that is sensitive to specific neurotransmitters. (2)
Recognition The ability to place an object in a category that gives it meaning—for example, recognizing a particular red object as a tomato. (1)
Recognition by components (RBC) theory Theory that states that objects are comprised of individual geometric components called *geons*, and we recognize objects based on the arrangement of those geons. (5)
Recognition profile The pattern of olfactory activation for an odorant, indicating which ORNs (olfactory receptor neurons) are activated by the odorant. (16)
Reflectance The percentage of light reflected from a surface. (9)
Reflectance curve A plot showing the percentage of light reflected from an object versus wavelength. (9)
Reflectance edge An edge between two areas where the reflectance of two surfaces changes. (9)
Refractive errors Errors that can affect the ability of the cornea and/or lens to focus incoming light onto the retina. (3)
Refractive myopia Myopia (nearsightedness) in which the cornea and/or the lens bends the light too much. *See also* **Axial myopia**. (3)
Refractory period The time period of about 1/1,000th of a second that a nerve fiber needs to recover from conducting a nerve impulse. No new nerve impulses can be generated in the fiber until the refractory period is over. (2)
Regularities in the environment Characteristics of the environment that occur regularly and in many different situations. (5)
Reichardt detector A neural circuit proposed by Werner Reichardt, in which signals caused by movement of a stimulus across the receptors are processed by a delay unit and an output unit so that signals are generated by movement in one direction but not in the opposite direction. (8)
Relative disparity The difference between two objects' absolute disparities. (10)
Relative height A monocular depth cue. Objects that have bases below the horizon appear to be farther away when they are higher in the field of view. Objects that have bases above the horizon appear to be farther away when they are lower in the field of view. (10)

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Relative size A cue for depth perception. When two objects are of equal size, the one that is farther away will take up less of the field of view. (10)

Representation, principle of A principle of perception that everything a person perceives is based not on direct contact with stimuli but on representations of stimuli on the receptors and in the person's nervous system. (1)

Representational momentum Occurs when motion depicted in a still picture continues in an observer's mind. (8)

Resolved harmonics Harmonics in a complex tone that create separated peaks in basilar membrane vibration, and so can be distinguished from one another. Usually lower harmonics of a complex tone. (11)

Resonance A mechanism that enhances the intensity of certain frequencies because of the reflection of sound waves in a closed tube. Resonance in the auditory canal enhances frequencies between about 2,000 and 5,000 Hz. (11)

Resonant frequency The frequency that is most strongly enhanced by resonance. The resonance frequency of a closed tube is determined by the length of the tube. (11)

Response compression The result when doubling the physical intensity of a stimulus less than doubles the subjective magnitude of the stimulus. (Appendix B)

Response criterion In a signal detection experiment, the subjective magnitude of a stimulus above which the participant will indicate that the stimulus is present. (Appendix C)

Response expansion The result when doubling the physical intensity of a stimulus more than doubles the subjective magnitude of the stimulus. (Appendix B)

Resting potential The difference in charge between the inside and the outside of the nerve fiber when the fiber is not conducting electrical signals. Most nerve fibers have resting potentials of about −70 mV, which means the inside of the fiber is negative relative to the outside. (2)

Resting-state fMRI The signal recorded using functional magnetic resonance imaging when the brain is not involved in a specific task. (2)

Resting-state functional connectivity A method in which resting-state fMRI is used to determine functional connectivity. (2)

Retina A complex network of cells that covers the inside back of the eye. These cells include the receptors, which generate an electrical signal in response to light, as well as the horizontal, bipolar, amacrine, and ganglion cells. (3)

Retinitis pigmentosa A retinal disease that causes a gradual loss of vision, beginning in the peripheral retina. (3)

Retinotopic map A map on a structure in the visual system, such as the lateral geniculate nucleus or the cortex, that indicates locations on the structure that correspond to locations on the retina. In retinotopic maps, locations adjacent to each other on the retina are usually represented by locations that are adjacent to each other on the structure. (4)

Retronasal route The opening from the oral cavity, through the nasal pharnyx, into the nasal cavity. This route is the basis for the way smell combines with taste to create flavor. (16)

Return to the tonic Occurs when a song begins with the tonic and ends with the tonic, where the tonic is the pitch associated with a composition's key. (13)

Reverberation time The time it takes for a sound produced in an enclosed space to decrease to 1/1,000th of its original pressure. (12)

Reversible figure–ground A figure–ground pattern that perceptually reverses as it is viewed, so that the figure becomes the ground and the ground becomes the figure. The best-known reversible figure–ground pattern is Rubin's vase–face pattern. (5)

Rhythm In music, the series of changes across time (a mixture of shorter and longer notes) in a temporal pattern. (13)

Rising phase of the action potential In the axon, or nerve fiber, the decrease in negativity from −70 mV to +40 mV (the peak action potential level) that occurs during the action potential. This increase is caused by an inflow of Na^+ ions into the axon. (2)

Rod A cylinder-shaped receptor in the retina that is responsible for vision at low levels of illumination. (3)

Rod–cone break The point on the dark adaptation curve at which vision shifts from cone vision to rod vision. (3)

Rod monochromat A person who has a retina in which the only functioning receptors are rods. (3)

Rod spectral sensitivity curve The curve plotting visual sensitivity versus wavelength for rod vision. This function is typically measured when the eye is dark adapted by a test light presented to the peripheral retina. (3)

Ruffini cylinder (SA2) A receptor structure in the skin associated with slowly adapting fibers. It has been proposed that the Ruffini cylinder is involved in perceiving "stretching." (15)

SA1 fiber Fiber in the skin associated with Merkel receptors that adapts slowly to stimulation and so responds continuously as long as a tactile stimulus is applied. (15)

SA2 fiber A slowly adapting fiber in the cutaneous system that is associated with the Ruffini cylinder and is located deeper in the skin than the SA1 fiber. This fiber also responds continuously to a tactile stimulus. (15)

Saccadic eye movement Rapid eye movement between fixations that occurs when scanning a scene. (6)

Saliency map A "map" of a visual display that takes into account characteristics of the display such as color, contrast, and orientation that are associated with capturing attention. (6)

Same-object advantage The faster responding that occurs when enhancement spreads within an object. Faster reaction times occur when a target is located within the object that is receiving the subject's attention, even if the subject is looking at another place within the object. (6)

Saturation (color) The relative amount of whiteness in a chromatic color. The less whiteness a color contains, the more saturated it is. (9)

Scale illusion An illusion that occurs when successive notes of a scale are presented alternately to the left and right ears. Even though each ear receives notes that jump up and down in frequency, smoothly ascending or descending scales are heard in each ear. Also called melodic channeling. (12)

Scene A view of a real-world environment that contains (a) background elements and (b) multiple objects that are organized in a meaningful way relative to each other and the background. (5)

Scene schema An observer's knowledge about what is contained in typical scenes. An observer's attention is affected by knowledge of what is usually found in the scene. (5)

Secondary olfactory area An area in the frontal lobe, near the eyes, that receives signals originating in the olfactory receptors. Also known as the orbitofrontal cortex. (16)

Secondary somatosensory cortex (S2) The area in the parietal lobe next to the primary somatosensory area (S1) that processes neural signals related to touch, temperature, and pain. (15)

Seed location Location on the brain that is involved in carrying out a specific task and which is used a reference point when measuring resting-state functional connectivity. (2)

Segregation The process of separating one area or object from another. *See also* **Figure–ground segregation**. (5)

Selective adaptation A procedure in which a person or animal is selectively exposed to one stimulus, and then the effect of this

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exposure is assessed by testing with a wide range of stimuli. Typically, sensitivity to the exposed stimulus is decreased. (4)

Selective attention Occurs when a person selectively focuses attention on a specific location or stimulus property. (6)

Selective rearing A procedure in which animals are reared in special environments. An example of selective rearing is the experiment in which kittens were reared in an environment of vertical stripes to determine the effect on orientation selectivity of cortical neurons. (4)

Selective reflection When an object reflects some wavelengths of the spectrum more than others. (9)

Selective transmission When some wavelengths pass through visually transparent objects or substances and others do not. Selective transmission is associated with the perception of chromatic color. *See also* **Selective reflection**. (9)

Semantic regularities Characteristics associated with the functions associated with different types of scenes. These characteristics are learned from experience. For example, most people are aware of the kinds of activities and objects that are usually associated with kitchens. (5)

Semitone The smallest interval in Western music—roughly the difference between two notes in a musical scale, such as between C and C#. There are 12 semitones in an octave. (13)

Sensation Often identified with elementary processes that occur at the beginning of a sensory system. *See also* **Structuralism**. (1)

Sensorimotor hearing loss Decrease in the ability to hear and perceive speech caused by damage to the hair cells in the cochlea. (14)

Sensory coding How neurons represent various characteristics of the environment. *See also* **Population coding**; **Sparse coding**; **Specificity coding**. (2)

Sensory component of pain Pain perception described with terms such as *throbbing*, *prickly*, *hot*, or *dull*. *See also* **Affective (emotional) component of pain**. (15)

Sensory receptors Cells specialized to respond to environmental energy, with each sensory system's receptors specialized to respond to a specific type of energy. (1)

Sensory-specific satiety The effect on perception of the odor associated with food eaten to satiety (the state of being satiated or "full"). For example, after eating bananas until satiety, the pleasantness rating for vanilla decreased slightly (but was still positive), but the rating for banana odor decreased much more and became negative. (16)

Sequential grouping In auditory scene analysis, grouping that occurs as sounds follow one another in time. (12)

Shadowing Listeners' repetition aloud of what they hear as they are hearing it. (6)

Shortest path constraint In the perception of apparent motion, the principle that apparent movement tends to occur along the shortest path between two stimuli. (8)

Signal The stimulus presented to a participant. A concept in signal detection theory. (Appendix C)

Signal detection approach An approach to detection of stimuli in which subjects' ability to detect stimuli is measured and analyzed in terms of hits and false alarms. This approach can take a subject's criterion into account in determining sensitivity to a stimulus. *See also* **Correct rejection**; **False alarm**; **Hit**; **Miss**; **Noise**; **Payoffs**; **Receiver operating characteristic (ROC) curve**; **Response criterion**; **Signal**. (Appendix C)

Similarity, principle of A Gestalt principle stating that similar things appear to be grouped together. (5)

Simple cortical cell A neuron in the visual cortex that responds best to bars of a particular orientation. (4)

Simplicity, principle of *See* **Pragnanz, principle of**. (5)

Simultaneous grouping The situation that occurs when sounds are perceptually grouped together because they occur simultaneously in time. (12)

Size constancy Occurs when the size of an object is perceived to remain the same even when it is viewed from different distances. (10)

Size–distance scaling A hypothesized mechanism that helps maintain size constancy by taking an object's perceived distance into account. According to this mechanism, an object's perceived size, S, is determined by multiplying the size of the retinal image, R, by the object's perceived distance, D. (10)

Size-weight illusion Erroneously predicting weight when observing two differently sized objects that have the same weight. The error occurs when the perceiver predicts that larger object will be heavier, and therefore uses more force to lift it, causing it to be lifted higher and to feel lighter. (7)

Slowly adapting (SA) fiber *See* **SA1 fiber**; **SA2 fiber**. (15)

Social pain Pain caused by negative social situations, such as rejection. (15)

Social touch One person touching another person. *See also* **interpersonal touching**. (15)

Social touch hypothesis Hypothesis that CT afferents and their central projections are responsible for social touch. (15)

Somatosensory receiving area (S1) An area in the parietal lobe that receives inputs from the skin and the viscera associated with somatic senses such as touch, temperature, and pain. *See also* **Primary somatosensory cortex (S1)**; **Secondary somatosensory cortex (S2)**. (15)

Somatosensory system The system that includes the cutaneous senses (senses involving the skin), proprioception (the sense of position of the limbs), and kinesthesis (sense of movement of the limbs). (15)

Sound (perceptual) The perceptual experience of hearing. The statement "I hear a sound" is using *sound* in this sense. (11)

Sound (physical) The physical stimulus for hearing. The statement "The sound's level was 10 dB" is using *sound* in this sense. (11)

Sound level The pressure of a sound stimulus, expressed in decibels. *See also* **Sound pressure level (SPL)**. (11)

Sound pressure level (SPL) A designation used to indicate that the reference pressure used for calculating a tone's decibel rating is set at 20 micropascals, near the threshold in the most sensitive frequency range for hearing. (11)

Sound spectrogram A plot showing the pattern of intensities and frequencies of a speech stimulus. (14)

Sound wave Pattern of pressure changes in a medium. Most of the sounds we hear are due to pressure changes in the air, although sound can be transmitted through water and solids as well. (11)

Sparse coding The idea that a particular object is represented by the firing of a relatively small number of neurons. (2)

Spatial attention Attention to a specific location. (6)

Spatial cue In tactile perception, information about the texture of a surface that is determined by the size, shape, and distribution of surface elements such as bumps and grooves. (15)

Spatial layout hypothesis Proposal that the parahippocampal cortex responds to the surface geometry or geometric layout of a scene. (5)

Spatial neglect Neurological condition in which patients with damage to one hemisphere of the brain do not attend to the opposite side of their visual world. (6)

Spatial updating Process by which people and animals keep track of their position within a surrounding environment when they move. (7)

Specificity coding Type of neural code in which different perceptions are signaled by activity in specific neurons. *See also* **Distributed coding**. (2)

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Spectral colors Colors that appear in the visible spectrum. *See also* **Nonspectral colors**. (9)

Spectral cue In hearing, the distribution of frequencies reaching the ear that are associated with specific locations of a sound. The differences in frequencies are caused by interaction of sound with the listener's head and pinnae. (12)

Spectral sensitivity The sensitivity of visual receptors to different parts of the visible spectrum. *See also* **Spectral sensitivity curve**. (3)

Spectral sensitivity curve The function relating a subject's sensitivity to light to the wavelength of the light. The spectral sensitivity curves for rod and cone vision indicate that the rods and cones are maximally sensitive at 500 nm and 560 nm, respectively. *See also* **Purkinje shift**. (3)

Speech segmentation The process of perceiving individual words from the continuous flow of the speech signal. (14)

Speech spectrograph Machine that records the time and frequency patterns of acoustic signals. Speech spectrograph or speech spectrogram also refers to the records created by this machine. (14)

Speechreading Process by which deaf people determine what people are saying by observing their lip and facial movements. (12)

Spinothalamic pathway One of the nerve pathways in the spinal cord that conducts nerve impulses from the skin to the somatosensory area of the thalamus. (15)

Spontaneous activity Nerve firing that occurs in the absence of environmental stimulation. (2)

Stapes The last of the three ossicles in the middle ear. It receives vibrations from the incus and transmits these vibrations to the oval window of the inner ear. (11)

Statistical learning The process of learning about transitional probabilities and other characteristics of the environment. Statistical learning for properties of language has been demonstrated in young infants. (14)

Stereocilia Thin processes that protrude from the tops of the hair cells in the cochlea that bend in response to pressure changes. (11)

Stereopsis The impression of depth that results from binocular disparity—the difference in the position of images of the same object on the retinas of the two eyes. (10)

Stereoscope A device that presents pictures to the left and the right eyes so that the binocular disparity a person would experience when viewing an actual scene is duplicated. The result is a convincing illusion of depth. (10)

Stereoscopic depth perception The perception of depth that is created by input from both eyes. *See also* **Binocular disparity**. (10)

Stereoscopic vision Two-eyed depth perception involving mechanisms that take into account differences in the images formed on the left and right eyes. (10)

Stevens's power law A law concerning the relationship between the physical intensity of a stimulus and the perception of the subjective magnitude of the stimulus. The law states that $P = KS^n$, where P is perceived magnitude, K is a constant, S is the stimulus intensity, and n is an exponent. (Appendix B)

Stimulus–behavior relationship The relationship between stimuli and behavioral responses, where behavioral responses can be perception, recognition, or action. (1)

Stimulus–physiology relationship The relationship between stimuli and physiological responses. (1)

Strabismus Misalignment of the eyes, such as crossed eyes or walleyes (outward looking eyes), in which the visual system suppresses vision in one of the eyes to avoid double vision, so the person sees the world with only one eye at a time. (10)

Striate cortex The visual receiving area of the cortex, located in the occipital lobe. (4)

Structural connectivity The structural "road map" of fibers connecting different areas of the brain. (2)

Structuralism The approach to psychology, prominent in the late 19th and early 20th centuries, that postulated that perceptions result from the summation of many elementary sensations. The Gestalt approach to perception was, in part, a reaction to structuralism. (5)

Subcortical structure Structure below the cerebral cortex. For example, the superior colliculus is a subcortical structure in the visual system. The cochlear nucleus and superior olivary nucleus are among the subcortical structures in the auditory system. (11)

Subtractive color mixture. *See* **Color mixture, subtractive**. (9)

Superior colliculus An area in the brain that is involved in controlling eye movements and other visual behaviors. This area receives about 10 percent of the ganglion cell fibers that leave the eye in the optic nerve. (4)

Superior olivary nucleus A nucleus along the auditory pathway from the cochlea to the auditory cortex. The superior olivary nucleus receives inputs from the cochlear nucleus. (11)

Surface texture The visual and tactile quality of a physical surface created by peaks and valleys. (15)

Sustentacular cell Cells that provide metabolic and structural support to the olfactory sensory neurons. (16)

Synapse A small space between the end of one neuron (the presynaptic neuron) and the cell body of another neuron (the postsynaptic neuron). (2)

Syncopation In music, when notes begin "off the beat" on the "and" count, which causes a "jumpiness" to the music. (13)

Syntax In language, grammatical rules that specify correct sentence construction. *See also* **Musical syntax**. (13)

Tactile acuity The smallest details that can be detected on the skin. (15)

Task-related fMRI fMRI measured as a person is engaged in a specific task. (2)

Taste The chemical sense that occurs when molecules—often associated with food—enter the mouth in solid or liquid form and stimulate receptors on the tongue. (16)

Taste bud A structure located within papillae on the tongue that contains the taste cells. (16)

Taste cell Cell located in taste buds that causes the transduction of chemical to electrical energy when chemicals contact receptor sites or channels located at the tip of this cell. (16)

Taste pore An opening in the taste bud through which the tips of taste cells protrude. When chemicals enter a taste pore, they stimulate the taste cells and result in transduction. (16)

Tectorial membrane A membrane that stretches the length of the cochlea and is located directly over the hair cells. Vibrations of the cochlear partition cause the tectorial membrane to bend the hair cells by rubbing against them. (11)

Temporal coding The connection between the frequency of a sound stimulus and the timing of the auditory nerve fiber firing. (11)

Temporal cue In tactile perception, information about the texture of a surface that is provided by the rate of vibrations that occur as we move our fingers across the surface. (15)

Temporal lobe A lobe on the side of the cortex that is the site of the cortical receiving area for hearing and the termination point for the ventral, or *what*, stream for visual processing. A number of areas in the temporal lobe, such as the fusiform face area and the extrastriate body area, serve functions related to perceiving and recognizing objects. (1)

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Temporal structure The time dimension of music, which consists of a regular beat, organization of the beat into measures (meter), and the time pattern created by the notes (rhythm). (13)

Test location Resting-state fMRI measured at a location other than the seed location. (2)

Texture gradient The visual pattern formed by a regularly textured surface that extends away from the observer. This pattern provides information for distance because the elements in a texture gradient appear smaller as distance from the observer increases. (10)

Threshold The minimum stimulus energy necessary for an observer to detect a stimulus. (1)

Tiling The adjacent (and often overlapping) location columns working together to cover the entire visual field (similar to covering a floor with tiles). (4)

Timbre The quality that distinguishes between two tones that sound different even though they have the same loudness, pitch, and duration. Differences in timbre are illustrated by the sounds made by different musical instruments. (11)

Tip links Structures at the tops of the cilia of auditory hair cells, which stretch or slacken as the cilia move, causing ion channels to open or close. (11)

Tonal hierarchy Ratings of how well notes fit in a scale. Notes that sound "right" in a scale would be high in the tonal hierarchy. Notes that don't sound like they fit in a scale are low in the hierarchy. (13)

Tonality Organizing pitches around the note associated with a composition's key. (13)

Tone chroma The perceptual similarity of notes separated by one or more octaves. (11)

Tone height The increase in pitch that occurs as frequency is increased. (11)

Tonic The key of a musical composition. (13)

Tonotopic map An ordered map of frequencies created by the responding of neurons within structures in the auditory system. There is a tonotopic map of neurons along the length of the cochlea, with neurons at the apex responding best to low frequencies and neurons at the base responding best to high frequencies. (11)

Top-down processing Processing that starts with the analysis of high-level information, such as the knowledge a person brings to a situation. Also called knowledge-based processing. Distinguished from bottom-up, or data-based processing, which is based on incoming data. (1)

Transcranial magnetic stimulation (TMS) Presenting a strong magnetic field to the head that temporarily disrupts the functioning of a specific area of the brain. (8)

Transduction In the senses, the transformation of environmental energy into electrical energy. For example, the retinal receptors transduce light energy into electrical energy. (1)

Transformation, principle of A principle of perception that stimuli and responses created by stimuli are transformed, or changed, between the environmental stimulus and perception. (1)

Transitional probabilities In language, the chances that one sound will follow another sound. Every language has transitional probabilities for different sounds. Part of learning a language involves learning about the transitional probabilities in that language. (14)

Transmission cell (T-cell) According to gate control theory, the cell that receives + and − inputs from cells in the dorsal horn. T-cell activity determines the perception of pain. (15)

Transmission curves Plots of the percentage of light transmitted through a liquid or object at each wavelength. (9)

Traveling wave In the auditory system, vibration of the basilar membrane in which the peak of the vibration travels from the base of the membrane to its apex. (11)

Trichromacy of color vision The idea that our perception of color is determined by the ratio of activity in three receptor mechanisms with different spectral sensitivities. (9)

Trichromat A person with normal color vision. Trichromats can match any wavelength in the spectrum by mixing three other wavelengths in various proportions. (9)

Triple meter In Western music, meter in which accents are in groups of three, such as 123 123 123, as in a waltz. (13)

Tritanopia A form of dichromatism in which a person is missing the short-wavelength pigment. A tritanope sees blue at short wavelengths, red at long wavelengths. (9)

Tuning curve, frequency *See* **Frequency tuning curve**. (11)

Tuning curve, orientation *See* **Orientation tuning curve**. (4)

Two-flash illusion An illusion that occurs when one flash of light is presented, accompanied by two rapidly presented tones. Presentation of the two tones causes the observer to perceive two flashes of light. (12)

Two-point threshold The smallest separation between two points on the skin that is perceived as two points; a measure of acuity on the skin. *See also* **Grating acuity**. (15)

Tympanic membrane A membrane at the end of the auditory canal that vibrates in response to vibrations of the air and transmits these vibrations to the ossicles in the middle ear. (11)

Unconscious inference The idea proposed by Helmholtz that some of our perceptions are the result of unconscious assumptions that we make about the environment. *See also* **Likelihood principle**. (5)

Uncrossed disparity Disparity that occurs when one object is being fixated, and is therefore on the horoptor, and another object is located behind the horoptor, farther from the observer. (10)

Uniform connectedness, principle of A modern Gestalt principle that states that connected regions of a visual stimulus are perceived as a single unit. (5)

Unilateral dichromat A person who has dichromatic vision in one eye and trichromatic vision in the other eye. People with this condition (which is extremely rare) have been tested to determine what colors dichromats perceive by asking them to compare the perceptions they experience with their dichromatic eye and their trichromatic eye. (9)

Unique hues Name given by Ewald Hering to what he proposed were the primary colors: red, yellow, green, and blue. (9)

Univariance, principle of Once a photon of light is absorbed by a visual pigment molecule, the identity of the light's wavelength is lost. This means that the receptor does not know the wavelength of the light that is absorbed, only the total amount of light it has absorbed. (9)

Unresolved harmonics Harmonics of a complex tone that can't be distinguished from one another because they are not indicated by separate peaks in the basilar membrane vibration. The higher harmonics of a tone are most likely to be unresolved. (11)

Value The light-to-dark dimension of color. (9)

Variability problem In speech perception, the fact that there is no simple relationship between a particular phoneme and the acoustic signal. (14)

Ventral pathway Pathway that conducts signals from the striate cortex to the temporal lobe. Also called the *what* pathway because it is involved in recognizing objects. (4)

Ventriloquism effect *See* **Visual capture**. (12)

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Ventrolateral nucleus Nucleus in the thalamus that receives signals from the cutaneous system. (15)

Vestibular system The mechanism in the inner ear that is responsible for balance and sensing the position of the body. (13)

Viewpoint invariance The condition in which object properties don't change when viewed from different angles. Responsible for our ability to recognize objects when viewed from different angles. (5)

Visible light The band of electromagnetic energy that activates the visual system and that, therefore, can be perceived. For humans, visible light has wavelengths between 400 and 700 nanometers. (3)

Visual acuity The ability to resolve small details. (3)

Visual angle The angle of an object relative to an observer's eyes. This angle can be determined by extending two lines from the eye—one to one end of an object and the other to the other end of the object. Because an object's visual angle is always determined relative to an observer, its visual angle changes as the distance between the object and the observer changes. (10)

Visual capture When sound is heard coming from a seen location, even though it is actually originating somewhere else. Also called the ventriloquism effect. (12)

Visual direction strategy A strategy used by moving observers to reach a destination by keeping their body oriented toward the target. (7)

Visual evoked potential An electrical response to visual stimulation recorded by the placement of disk electrodes on the back of the head. This potential reflects the activity of a large population of neurons in the visual cortex. (3)

Visual form agnosia The inability to recognize objects. (1)

Visual masking stimulus A visual pattern that, when presented immediately after a visual stimulus, decreases a person's ability to perceive the stimulus. This stops the persistence of vision and therefore limits the effective duration of the stimulus. (5)

Visual pigment A light-sensitive molecule contained in the rod and cone outer segments. The reaction of this molecule to light results in the generation of an electrical response in the receptors. (3)

Visual pigment bleaching The change in the color of a visual pigment that occurs when visual pigment molecules are isomerized by exposure to light. (3)

Visual pigment regeneration Occurs after the visual pigment's two components—opsin and retinal—have become separated due to the action of light. Regeneration, which occurs in the dark, involves a rejoining of these two components to reform the visual pigment molecule. This process depends on enzymes located in the pigment epithelium. (3)

Visual receiving area The area of the occipital lobe where signals from the retina and LGN first reach the cortex. (4)

Visual salience Characteristics such as bright colors, high contrast, and highly visible orientations that cause stimuli to stand out and therefore attract attention. (6)

Visual search A procedure in which a person's task is to find a particular element in a display that contains a number of elements. (6)

Visuomotor grip cell A neuron that initially responds when a specific object is seen and then also responds as a hand grasps the same object. (7)

Voice cells Neurons in the temporal lobe that respond more strongly to same-species voices than to calls of other animals or to "non-voice" sounds. (14)

Voice onset time (VOT) In speech production, the time delay between the beginning of a sound and the beginning of the vibration of the vocal chords. (14)

Waterfall illusion An aftereffect of movement that occurs after viewing a stimulus moving in one direction, such as a waterfall. Viewing the waterfall makes other objects appear to move in the opposite direction. *See also* **Movement aftereffect**. (8)

Wavelength For light energy, the distance between one peak of a light wave and the next peak. (3)

Wayfinding The process of navigating through the environment. Wayfinding involves perceiving objects in the environment, remembering objects and their relation to the overall scene, and knowing when to turn and in what direction. (7)

Weber fraction The ratio of the difference threshold to the value of the standard stimulus in Weber's law. (Appendix A)

Weber's law A law stating that the ratio of the difference threshold (*DL*) to the value of the stimulus (*S*) is constant. According to this relationship, doubling the value of a stimulus will cause a doubling of the difference threshold. The ratio *DL/S* is called the Weber fraction. (Appendix A)

Wernicke's aphasia An inability to comprehend words or arrange sounds into coherent speech, caused by damage to Wernicke's area. (14)

Wernicke's area An area in the temporal lobe involved in speech perception. Damage to this area causes Wernicke's aphasia, which is characterized by difficulty in understanding speech. (2)

***What* pathway** *See* **Ventral pathway**. (4)

***What* pathway, auditory** Pathway that extends from the anterior belt to the front of the temporal lobe and then to the frontal cortex. This pathway is responsible for perceiving complex sounds and patterns of sounds. (12)

***Where* pathway** *See* **Dorsal pathway**. (4)

***Where* pathway, auditory** Pathway that extends from the posterior belt to the parietal lobe and then to the frontal cortex. This pathway is responsible for localizing sounds. (12)

Word deafness Occurs in the most extreme form of Wernicke's aphasia, when a person cannot recognize words, even though the ability to hear pure tones remains intact. (14)

Young-Helmholtz theory *See* **Trichromacy of color vision**. (9)

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